DOCTORAL DISSERTATION

# INTERPRETATION OF THIRD-PARTY SOCIAL INTERACTION IN DOGS

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# CONTENT

# ÖSSZEFOGLALÓ

A harmadik-felek közötti szociális interakciók értelmezésének vizsgálata információval szolgál arról, hogy az állatok hogyan kezelik azokat a helyzeteket, amikor nem érhető el közvetlen információ a szociális környezetükkel kapcsolatban, vagy a közvetlen interakció során történő információszerzésnek magas a költsége. Bár a szociális hallgatózást számos fajnál vizsgálták, a tanulmányok közti lényeges különbségek miatt nehéz összehasonlító szempontból következtetéseket levonni. Egy másik probléma, hogy a legtöbb esetben nincs információ arról, hogy az egyes fajok viselkedését befolyásolja-e harmadik-felek közötti interakciók során szerzett információ, különböző helyzetekben. A disszertációban három különböző kutatási területen (*szociális kiértékelés*, *féltékenység* és *élőség észlelés*) vizsgáltuk, hogy a kutyák megfigyelnek-e harmadik-felek közötti interakciókat, valamint a közvetett interakció során gyűjtött információ befolyásolja-e viselkedésüket. A szociális kiértékelést csak elméleti szempontból vizsgáltuk, azonban különböző viselkedéstesztekben tanulmányoztuk, hogy a kutyák miképp viselkednek ismerős szociális partnerek közti interakció során (értékes szociális partnerért folyó kompetíció, azaz féltékeny viselkedés megjelenése), valamint a kutyák (és felnőtt emberek) hogyan reagálnak élettelen ágensek közti interakciókra (élőként való észlelés). A szociális kiértékeléssel kapcsolatban leírtunk egy általános kutatási keretet, ami elősegítheti a témával kapcsolatos jövőbeni összehasonlító kutatásokat, rámutattunk a kutatásban felmerülő problémákra, valamint felvetettük ezek lehetséges megoldásait. A kísérletes kutatásunk alapján az emberhez hasonlóan kutyák is hajlamosak élőként észlelni élettelen ágenseket csupán azok mozgása alapján, kiértékelni harmadik-felek közti lehetséges kapcsolatot (pl. egymástól függő vagy független mozgás vagy a fontos szociális partner és egy másik ágens közti interakció veszélyezteti-e a kapcsolatot), és felhasználni ezt az információt, amikor közvetlen interakcióba kerülnek a megfigyelt ágensekkel (pl. nagyobb érdeklődés egy élő, mint egy élettelen ágens irányába vagy a kapcsolat fenntartását elősegítő viselkedés mutatása). Tehát a kutyák képesek figyelembe venni harmadik-felek közti interakciókból származó információt, legalább két különböző helyzetben. A harmadik-felek közti szociális interakciókból származó információ felhasználásának képessége mind rátermettség, mind túlélés szempontjából fontos lehet, különböző helyzetekben. Azonban továbbra is nyitott kérdés, hogy a különböző helyzetekben (vagy különböző fajoknál) megjelenő szociális hallgatózás azonos mentális mechanizmuson alapul-e.

# ABSTRACT

Investigating the interpretation of third-party social interactions provide information on how human and non-human animals handle their social environment when direct information is not available or obtaining information through direct encounter has high cost. Social eavesdropping has been investigated in several species, but substantial differences between studies hinders between-species comparisons. We also lack information on whether the behaviour of different species is influenced by information gathered in third-party social interactions in different contexts. In the dissertation we used three different research topics (*social evaluation*, *jealousy* and *perceptual animacy*) to study whether dogs are attentive in third-party contexts and whether their behaviour is influenced by the information gathered in third-party interactions. We investigated social evaluation from a theoretical point of view and conducted experiments with dogs to study how they behave in indirect interactions with familiar social partners (competition for valuable social partner, i.e. jealous behaviour), and how dogs (and adult humans) react in third-party interactions with inanimate agents (recognition of animacy). We developed a general framework for social evaluation to facilitate future comparative research on the topic, and we point out possible problems in research and provide solutions to these issues. In our experimental research we found, that dogs, similarly to humans, tend to perceive inanimate agents as animate based on simple motion cues, evaluate possible relationship between third-party agents (e.g. dependency or independency in their movement, or whether the interaction of the valued social partner and another agent threatens the relationship), and use this information to direct their future behaviour accordingly toward these agents (e.g. higher interest in animate, than in inanimate agents or displaying behaviour that facilitate to maintain the important social relationship). Thus dogs are able to take into consideration information gathered in third-party social interactions in at least two different situations. The ability to apply information gathered in third-party social interactions can contribute to fitness and survival in different contexts; however, it is still an open question whether social eavesdropping in different contexts (and species) relies on the same mental mechanisms.

”*The ongoing fragmentation of knowledge and resulting chaos in philosophy are not reflections of the real world but artifacts of scholarships.*”

– Wilson, 1998 (p 8)

# 1. INTRODUCTION

Individuals of many species form temporary or permanent groups. Living closely to conspecifics provide the advantage of higher vigilance to predators or cooperating over tasks (e.g. hunting or cooperative breeding); however, competition over resources (including the mate) also increases. Within a group it is important to have knowledge about other individuals regarding their behaviour, rank in hierarchy or their social relationships (kinship, mates or allies), etc. (e.g. Cheney and Seyfarth 2004; Peake 2004). Thus gaining information through not only direct, but indirect (third-party) interactions is beneficial (e.g. Cheney and Seyfarth 2004; Peake 2004; Abdai and Miklósi 2016). It should also be noted that information about conspecifics may be important to solitary species as well (e.g. territoriality; see below).

Information gathered in direct interaction provides more accurate predictions about others' future behaviour and about the possible outcome of interacting with them, but it may not be the best strategy. Engaging in direct interaction can have high cost regarding survival and fitness, and we should also consider that as group size increases, it becomes more difficult to have face-to-face interactions with all members. Also, in case of dynamic changes within the group (e.g. rank in hierarchy when it is based on age or size; Cheney and Seyfarth 2004) it would be difficult to be updated via direct interactions only. Thus learning about others by observing an interaction between two or more individuals can be advantageous. However, this type of social information may be more difficult to handle cognitively, and it is less accurate due to the possible lack of information about the previous encounters among the individuals, their social relationships and rules present in the group (Abdai and Miklósi 2016).

Eavesdropping in its broadest sense is when an individual other than the primary target uses the information of a signal from a communicative interaction, and subsequently changes its behaviour toward the individuals involved (e.g. Peake 2004; Bonnie and Earley 2007). Two types of eavesdropping have been differentiated (e.g. Peake 2004; Bonnie and Earley 2007). *Interceptive eavesdropping* is when the individual intercepts the signal itself (absolute information), for example, convict cichlids (*Cichlasoma nigrofasciatum*) attend to the alarm signals of others, the primary targets of which are the relatives of the signaller (Shennan et al. 1994). In the case of *social eavesdropping* the individual obtains information from the interaction between others that cannot be gained solely from the signal (relative information), for example, male great tits (*Parus major*) show different behaviour toward intruders depending on their status (higher or lower), based on information obtained from the intruder's interaction

with another male familiar to the subject (Peake et al. 2002). Here our main concern is information gathering in third-party social interactions via social eavesdropping, but it should be noted that in many cases it is (almost) impossible to clearly separate the two. By definition, social eavesdropping occurs in communicative interactions when the observer attends to signals, but not cues (Bonnie and Earley 2007); however, we suggest that social eavesdropping should be broadened to include non-communicative interactions and the possibility that the obtained information is based on cues (only if cues are present due to the interaction). For example, in the "hill-paradigm" presented to human infants to study social evaluation (Hamlin et al. 2007; Hamlin 2015; see Section 2.6.1), an agent helps to another to move toward its goal without engaging in communication. In this scenario there is no signal exchange between the agents, but based on the behaviour infants can infer the future behaviour of at least one of the individuals (note that the identity of the other can be important as well, see Hamlin et al. 2011).

The ability to eavesdrop on third-party social interactions have been investigated in different contexts in non-human and human species. In *fish*, the main focus has been on mate choice and eavesdropping on visual displays in male-male interactions (e.g. Siamese fighting fish (*Betta splendens*), Doutrelant and McGregor 2000; green swordtails (*Xiphophorus helleri*), Earley and Dugatkin 2002), but there is a growing body of studies about social eavesdropping in cleaner-client fish interactions as well (e.g. Bshary 2002; Tebbich et al. 2002; Bshary and Grutter 2006). In *birds*, researchers mainly investigated the ability of individuals to obtain information about others that may intrude on their territory, and conducted research on mate choice copying (e.g. great tits, (Peake et al. 2002); Japanese quails (*Coturnix coturnix japonica*), Galef and White 1998). However, mate choice copying has been connected to not only social eavesdropping, but social learning and public information use as well (see Bonnie and Earley 2007). In *non-human primates*, the ability to infer third-party social relationships has been studied most widely (e.g. vervet monkeys (*Chlorocebus aethiops*), Cheney and Seyfarth 1980; yellow baboons (*Papio cynocephalus*) Cheney et al. 1995). Recently social evaluation in third-party social interactions has also been studied in dogs (*Canis familiaris*) (e.g. Marshall-Pescini et al. 2011; Freidin et al. 2013), non-human primates (e.g. Russell et al. 2008; Herrmann et al. 2013) and humans (e.g. Hamlin et al. 2007; Dahl et al. 2013); but procedural designs differed in significant ways among these studies (for a review see Abdai and Miklósi 2016).

In relation to the recognition of third-party social relationships, Cheney & Seyfarth (2004) raised that differences between species regarding social eavesdropping are possibly due to the different social context it occurs (ecological relevance), and not based on their cognitive abilities (for other hypotheses see Cheney and Seyfarth 2004). In contrast, Subiaul et al. (2008)

suggested (specifically) in case of reputation judgment, that when reputation judgment occurs in only one context in the specific species, the skill is more likely to be driven by domain-specific mechanism that processes the information regarding the specific context only. They argued that due to its inflexibility, this phenomenon is only analogously similar to reputation judgment (e.g. in fish and birds; see Subiaul et al. 2008). We propose that based on current literature, we do not have enough information to conclude whether specific species eavesdrop on others only in one context, or it is the artefact of lack of testing in other situations. Further, without knowing whether there are similarities and/or differences among the underlying cognitive mechanisms driving this (or these) skill(s), we can draw false conclusions. Thus we argue that the main question should be whether there is a difference between social eavesdropping occurring in different contexts, or difference between species when they eavesdrop in (functionally) similar contexts.

Thus information gathering in third-party interactions via social eavesdropping occurs in different contexts and there is a debate on whether the underlying cognitive mechanism differs in these cases, and whether this skill can be generalized to different contexts within species. The information obtained can be highly different, from detecting the state of agent (animate vs. inanimate), through observing their behaviour (to predict their future behaviour), to identifying the relationship among agents involved in the interaction. In the present dissertation, we investigated in three different research topics whether dogs are attentive in third-party context and whether their behaviour is influenced by the information gathered in third-party interactions. We investigated social evaluation from a theoretical point of view in order to facilitate future comparative research on this emerging topic. We conducted experiments with dogs to study how they behave in indirect interactions with familiar social partners (competition for valuable social partner, i.e. jealous behaviour), and how dogs (and adult humans) react in third-party interactions with unfamiliar inanimate agents (recognition of animacy). These three topics cover areas in which social eavesdropping may occur in a wide range of animal species (of course other situations, for example, rank in hierarchy or mate choice should be also important to investigate from a comparative point of view). By testing the same species in different contexts we may get an insight in the domain-specificity of social eavesdropping (cf. Subiaul et al. 2008). Considering the importance of these experiments within their respective research fields (*social evaluation, jealousy* and *perceptual animacy*) (regardless of whether they are studied within the framework of third-party social interaction), I will discuss them in the following chapters by focusing on their own respective fields, and I discuss our findings in light of third-party social interaction only in the last chapter (Chapter 5 and 6).

## 1.1. Aims

*Social evaluation* is an important cognitive capacity that has gained great attention in the past decade due to its supposed relation to morality (e.g. Sheskin and Santos 2012; Hamlin 2013). However, across studies many different but functionally similar concepts are applied, and comparative investigation is hindered by methodological discrepancies. In our review of social evaluation the aim was to (1) provide a general framework to study social evaluation in order to facilitate future comparative research; (2) use an ethological approach to the phenomenon (Tinbergen's four questions: function, mechanism, development and evolution; Tinbergen 1951); (3) review the experimental works that we have found to describe the same phenomenon, and discuss these from the viewpoint of our framework; and (4) point out possible problems in research and provide solutions.

For the experimental testing of third party interaction we studied the '*jealous behaviour'* in dogs. Jealousy in humans is an important secondary emotion that has been investigated in several social relationships, mostly in romantic and parent-filial relationships (for reviews see e.g. Harris 2003; Hart 2016). However, little is known about its evolutionary background and the underlying cognitive mechanisms. Here our aim was to find out whether dogs show jealous behaviour in similar situation that elicits this behaviour in human children. The emergence of jealous behaviour requires dogs to assess the situation correctly (whether the relationship is threatened by the other agent), thus we further gain information on their ability to take into consideration third-party social interactions.

The above phenomena are both fairly complex, but it is also important to investigate the interpretation of third-party social interactions on a more basic, mechanistic level. *Perceptual animacy* is a widely studied phenomenon in humans, but comparisons with non-human species are neglected. There are many important theoretical debates about the phenomenon, and it can also serve as a *tool* for other research areas (e.g. research on autism spectrum disorder; Abell et al. 2000; Rutherford et al. 2006). By studying animacy perception, (1) we aimed to compare human and non-human species because this provided us with important insights about the phenomenon. (2) We have also developed a novel method that may facilitate comparative studies, considering that current methods (displaying videos) are not necessarily appropriate to apply in non-human species.

# 2. SOCIAL EVALUATION

In gregarious species the recognition of conspecifics as prosocial or antisocial is important to predict the future behaviour of others. The mental process underlying this skill enables the avoidance of harmful individuals and facilitate the choice of an appropriate partner to cooperate with. This mental process has been referred to in different species as reputation formation or reputation judgment (Subiaul et al. 2008; Herrmann et al. 2013), image scoring (Bshary and Grutter 2006; Russell et al. 2008), social evaluation (Hamlin et al. 2007; Anderson et al. 2013a) or simply described as social eavesdropping (Marshall-Pescini et al. 2011; Freidin et al. 2013). In conclusion, different authors from different areas use related concepts to describe similar phenomena that probably have similar function in the different species. Although social evaluation can emerge in direct and indirect interactions as well, here we focused more on the latter issue.

After describing a general framework, we visited the phenomenon from the viewpoint of Tinbergen's four questions (function, mechanism, development and evolution) (Tinbergen 1951). For this, we focused on the phenomenon itself, without the influence of current results that may help us to evaluate these studies more objectively later.

## 2.1. General framework

Social evaluation is a mental process during which an individual (1) assigns different values (positive or negative) to particular behavioural patterns (e.g. helping or hindering) that are performed in a social interaction (e.g. problem solving), (2) associates these behaviours and the assigned values with specific individuals (partnership values), and (3) display different behaviours (e.g. preference or avoidance) toward others based on the overall value which has been associated with them. It is composed of two building blocks: negativity and positivity bias. Negativity bias is the aversion to negative (social) stimuli that drives the avoidance of antisocial individuals (Hamlin et al. 2010; Anderson et al. 2013a). In contrast, positivity bias refers to the preference toward positive (social) stimuli that manifest in the preference toward prosocial individuals (Hamlin et al. 2007). These terms can be used more widely; however, here we refer to them only within a cooperative framework. Although other features of a potential partner are also important when choosing an individual to engage in cooperation (for example, its

skilfulness; Melis et al. 2006), we argue that these can be discussed independently and we focus solely on social evaluation.

In the simplest case, an individual can be faced with a choice between prosocial vs. antisocial, prosocial vs. neutral or neutral vs. antisocial individuals. In general, we expect the choice of the relatively prosocial partner due to the consequences of an inaccurate choice; however, the presence of only one of the two building blocks may lead to different choice response. In case of positivity bias a preference toward the relatively positive partner is expected in all scenarios (prosocial partners in the first two and neutral partner in the third scenario); while the presence of only negativity bias would lead to an avoidance of the negative partner only, which would result in no choice between the prosocial vs. neutral individuals. In former studies, authors used the term social evaluation irrespectively of whether both positivity and negativity bias are present or only one of them (see e.g. Anderson et al. 2013). In contrast, we suggest that the term should be restricted to cases when both of them are present due to the functional, and potential developmental and evolutionary differences between them (see below). We assume that positivity and negativity bias emerge independently from each other and merge into a unified system only later, which we refer to as social evaluation. As a unified cognitive capacity it cumulates both negative and positive partnership values and the behaviour of the individual is driven by the overall partnership value that has been associated with the other individual.

## 2.2. The function of social evaluation

### 2.2.1. Function of negativity bias

Aversion to negative stimuli in general enhances survival; including stimuli that relate to social interactions. For example, capuchin monkeys (*Cebus apella*) regularly cooperate with the members of their group and show prosocial behaviour as well (de Waal et al. 1993; Mendres and De Waal 2000). Thus it can be assumed that factors that help to maintain long-term cooperation, or for example, discrimination against cheaters should be present (Trivers 1971). This assumption is in line with the results of Anderson et al. (2013) who found that capuchin monkeys show aversion to antisocial human partners in laboratory setting.

Considering that engaging in any interaction with an antisocial partner can have high cost, we assume that depending on the extent of cost, in specific cases it is advantageous to avoid not only known antisocial partners, but partners with unknown partnership values as well. Thus in

situations in which the cost of choosing an antisocial partner outweighs the advantage that can be gained from interacting with a prosocial partner, we expect the avoidance of unfamiliar individuals (higher risk). However, if the benefit is higher than the cost, it worth to try to solicit the help of unfamiliar individuals even though it is risky (lower risk). For example, in bluestreak cleaner wrasses (*Labroides dimidiatus*) and their client reef fishes, it is more advantageous to the client to choose the known cleaner rather than an unknown one (Bshary and Grutter 2006; see the details later).

### 2.2.2. Function of positivity bias

In most cases failing to choose the more prosocial partner has lower cost than erroneously choosing an antisocial one; however, in long-term groups there may be a selection for the preference for prosocial individuals. In human infants it seems that positivity bias develops between the age of three and six months (Hamlin et al. 2007, 2010); however, in non-human species we do not have information about the presence of it, due to the lack of comparison of prosocial/antisocial partner with a neutral partner (but see Anderson et al. 2013). Interestingly, Anderson et al. (2013) did not find evidence on positivity bias in capuchin monkeys, despite they are known to be a cooperative species. However, considering that capuchins are well-documented to be prosocial maybe the discrimination against antisocial individuals is sufficient, but there has not been high selective pressure on being able to prefer prosocial others. Thus we expect that positivity bias might be present in species in which there is a higher variability among individuals regarding their level of prosociality.

## 2.3. Cognitive mechanisms in social evaluation

To date, there is lack of data on the underlying mechanisms of social evaluation. Based on the current literature, it is difficult to determine the cues, which social evaluation is based on, and the decision rules that provide the basis of computations. For example, does negative or positive partnership values are considered with equal strength? Do kinship and familiarity have an effect on individual biases? Unfortunately, we cannot answer these types of questions at the moment. Thus we argue that working definitions should not be based on hypothetical differences among the underlying cognitive mechanisms of the phenomena under investigation (see Subiaul et al. 2008).

## 2.4. The development of social evaluation

As we raised earlier, we propose that negativity and positivity bias emerge independently during development and become a unified cognitive capacity only later. We assume that due to its importance in survival, negativity bias develops relatively early, but positivity bias, may not have a function at this age. Learning about antisocial and prosocial tendencies of others may be facilitated by genetic predispositions, which may be more emphasized in case of negativity bias due to its importance in survival. For example, Sackett (1966) found that rhesus macaques (*Macaca mulatta*) at the age of two months already discriminate the picture of a threatening monkey from others, displaying disturbance behaviour (rocking, huddling, self-clasping, fear and withdrawal). This suggest that aversion to negative social stimuli is present even without previous experience at an early age (see also aversion to antisocial partner in three-month-old infants; Hamlin et al. 2010).

The development of the ability to eavesdrop on third-party interactions also should be considered here. Direct interactions have a significant effect on individuals because the outcome of other's behaviour is more unequivocal in these situations. These experiences may facilitate processing information in third-party interactions.

## 2.5. The evolution of social evaluation

The evolution of cooperation puzzled many researchers in the past decades (Axelrod and Hamilton 1981; Dugatkin 1997; Sachs et al. 2004; Nowak 2007), considering that evolution is based on the survival of the fittest and individuals compete with each other, yet cooperation is widespread in the animal kingdom. There have been multiple mechanisms suggested for the evolution of cooperation, and different authors tend to describe partially different mechanisms (for a review see West et al. 2007). Despite the differences between these mechanisms, they all can be described by the cost-benefit ratio of cooperation and defection. To date there is no information about how kinship influences social evaluation, but for example, from the viewpoint of individual selection (e.g. Sachs et al. 2004) and (direct, indirect and network) reciprocity (e.g. Nowak 2007) the ability to associate partnership values to others would possibly be advantageous. However, social evaluation requires individual recognition and memories of past interactions (see also reciprocal altruism; Brosnan and De Waal 2002; Schino and Aureli 2009).

## 2.6. Comparative approach to social evaluation

In the following, we review experimental studies which we have identified as tackling the same phenomenon, despite the fact that they may have been put forward on different theoretical basis and utilize different terminology.

### 2.6.1. Social evaluation in human infants

In a series of studies, Hamlin et al. (e.g. 2007, 2010, 2011) investigated whether human infants show different behaviour toward prosocial and antisocial partners. Researchers used different inanimate agents (geometrical shapes or hand puppets) as social partners and presented an interaction between them to the infants. In these scenes a recipient needed help to reach a goal (e.g. get to the top of a hill, get open a box, etc.) and interacted with either a prosocial (helper), an antisocial (hinderer), or a neutral agent. In their first study, Hamlin et al. (2007) investigated whether infants of 6 and 10 months of age show some behavioural evidence for social evaluation. Infants observed an inanimate object trying to go up a hill and failing twice, and then another agent entered the scene. Based on their role the partner helped or hindered the recipient to reach its goal, and the neutral partner moved uphill or downhill without engaging in an interaction. Infants of both age groups chose the prosocial partner over the antisocial and the neutral agent, and before reaching for the partner they looked longer at the prosocial than at the antisocial agent (see Hamlin et al. 2010). These results suggested that infants as young as 6 months are able to socially evaluate others in a cooperative context.

Some authors raised concerns about the method used by Hamlin et al. (2007) and argued that some aspects of the procedure might have influenced infants' choice preference (Scarf et al. 2012; but see Hamlin 2015). However, Hamlin and Wynn (2011) obtained similar results in infants of different ages in other situations played with hand puppets in front of the subjects. In one of the experiments, in the observed scene, the recipient tried to open a box to obtain the toy from inside, but failed. Then either a prosocial partner helped to open the box or an antisocial agent shut it hindering the recipient to obtain the toy. In the other experiment, infants saw an agent playing with a ball and dropping it accidentally in the direction of one of two agents. After the agent grabbed the ball, the recipient asked for it. The prosocial agent gave it back to the recipient, but the antisocial partner took it offstage. In the first experiment, they found that infants of 5 and 9 months of age choose the prosocial partner over the antisocial one, and found the same choice preference in 5-month-old infants in the latter experiment as well. They also

found that infants of 3 months of age look longer ('preferential looking') at the prosocial than at the antisocial agent in the social condition. However, in these cases a neutral partner was never introduced to the subjects, thus we do not know whether the observed discrimination between the agents was due to negativity and/or positivity bias.

In another study, Hamlin et al. (2011) used similar procedure to test selective social evaluation in 5- and 8-month-old infants, i.e. whether the evaluation of others as prosocial or antisocial depends on the relative social roles played by the partners (relative partnership values). In this case subjects observed the toy-in-the-box scene described previously, and then the ball-dropping play, but with the former prosocial or antisocial individual as the recipient. Authors found that while 5-month-old infants choose the prosocial partner in both cases, regardless of the role of the recipient in the toy-in-the-box scene, 8-month-olds chose the antisocial partner, the partner that behaved antisocially toward an antisocial agent. Their results suggested that although younger infants only take into account the outcome of the interaction between third-parties, at least from 8 months of age they are able to evaluate the observed interactions globally.

Hamlin (2013b) also tested whether 5- and 8-month-old infants are able to evaluate others based solely on their behaviour, and not the outcome of their actions. In this study, they presented different scenarios to the subjects by presenting hand puppets in front of the infants as in previous studies. In the first experiment, the valence of the partners was different, but the outcome was the same from the viewpoint of the recipient (successful helper vs. failed hinderer; failed helper vs. successful hinderer). In the second experiment, the partners were a failed helper and a failed hinderer, thus the outcomes of their actions were contradictory with their individual social attitudes (e.g. failed hinderer is antisocial, but the outcome is positive). In the third case, they presented interactions in which the two partners had the same status, however, the outcomes were different (e.g. successful helper vs. failed helper). In all experiments infants could choose between the partners (two puppets) presented to them after the display. Only 8-month-old infants distinguished between the partners in the different experiments based on their behaviour and not simply the positive or negative outcome of their actions, meaning that they chose the prosocial partner over the antisocial one. However, Hamlin (2014) later found that when enough time is given to 5-month-old infants to process the interactions, they are also able to take into account the context in the evaluation of others.

The above results suggest that social evaluation emerges in at least 5–6 months old human infants, and one study showed that 3-month-olds also show preference toward the prosocial agent over the antisocial (Hamlin and Wynn 2011). So far, only one study investigated whether

at 3 months of age positivity and/or negativity bias can be detected in infants. Hamlin et al. (2010) presented the 'hill paradigm' (see above; Hamlin et al. 2007) to 3-month-old infants and used preferential looking to measure whether they discriminate among prosocial, antisocial and neutral agents. They found that infants this young looked longer at the prosocial than at the antisocial partner, however, they did not differentiate between the prosocial and the neutral agents. In contrast, they looked four times longer at the neutral than at the antisocial partner. Although a few months later infants show preference toward a prosocial agent (Hamlin et al. 2007) and apparently are able to take into account contextual information as well (Hamlin et al. 2011), at 3 months of age negativity, but not positivity bias can be detected. Based on this result authors concluded that the ability to socially evaluate others is a fundamental capacity; however, according to our criterion without the emergence of positivity bias this cannot be considered as social evaluation.

There was only one study in which researchers used a 'sharing' situation as the observed interaction in human infants (Herrmann et al. 2013). This is unfortunate from the comparative viewpoint because in non-human species researchers mainly used this particular situation to test social evaluation ability (e.g. Russell et al. 2008; Marshall-Pescini et al. 2011). Herrmann et al. (2013) first tested 30-month-old toddlers in direct interaction with two human partners, and later presented a third-party interaction involving the same two humans now behaving toward a recipient. The human partner was either prosocial and tried to give a ball to the recipient (the toddler in the direct and an adult human in the indirect interaction), or antisocial who prevented the transfer by the prosocial human. Then both partners offered a ball to the toddler who could reach for one of them. The same moment the toddler reached for the ball, the partners withdrew their hands. The researchers found that after engaging in direct interaction with the partners, toddlers show preference toward the prosocial human, while after watching the third-party interaction they did not show preference toward either of the partners. Note, however, that in the latter case they had negative direct experience at choice (both humans withdrew their hands when the toddler reached for the ball) which probably had greater influence than evaluating them based on their behaviour toward others. Thus, we cannot separate the effect of direct experiences with the partners from the results in the third-party interaction. It is also worth to note that although these results suggest that 30-month-old toddlers have difficulties in discriminating between prosocial and antisocial others in a third-party interaction, Hamlin et al. (2007, 2011) and Hamlin (2013b) found that infants as young as 5-6 months of age discriminate between prosocial and antisocial partners.

Hamlin et al. (2011) also tested 19- to 24-month-old toddlers in the box-opening and ball-playing scenario with hand puppets as partners. In this case, in the test phase toddlers either got one treat to give it to one of the partners or had to take one treat from one of the partners. They found that toddlers of both ages gave the treat to the prosocial partner and took one from the antisocial one. Another research group found different results as Hamlin et al. (2011) when using adult humans as partners, in a similar set up as the ball-playing scenario (Dahl et al. 2013). In this study, 17-, 22-, and 26-month-old toddlers observed an interaction between three humans. The experimenter (recipient) invited the partners to play and rolled them a ball. After the recipient asked them to roll it back, the prosocial partner did at request, but the antisocial human put it away. In the test phase the two partners both tried to reach the same object and the infants were allowed to help them. Dahl et al. (2013) found that infants of 17 and 22 months of age help equally often to the partners, and only at the age of 26 months they prefer to help to the prosocial partner over the antisocial human.

The results of the studies by Hamlin et al. (2010, 2011) and Hamlin (2013b) suggest a developmental timescale of social evaluation in human infants: first only negativity bias can be detected, and at around 5–6 months of age positivity bias emerges as well, making the functioning of a social evaluation system complete. However, based on the results of Dahl et al. (2013) and Herrmann et al. (2013) we should be careful to draw conclusions about the functionality of this system at a very young age. However, there are main differences between the studies described above. Hamlin et al. (2007, 2011) used inanimate objects as partners and presented different helping situations to infants of different ages, while the other two research groups tested older infants, and used humans as partners. Furthermore, Herrmann et al. (2013) used a sharing situation instead of the helping scenario. Thus methodological differences across studies could be responsible for these divergent findings (see below).

Recently, Salvadori et al. (2015) attempted to reproduce the study of Hamlin and Wynn (2011) by using the same procedure with slight modifications, but they failed to find the same results. Although such studies (Dahl et al. 2013; Herrmann et al. 2013; Salvadori et al. 2015) weaken the findings of Hamlin et al. (2007) and Hamlin and Wynn (2011), it should be take into consideration that the latter group found similar behaviour in different contexts in children of different ages. However, there is a need for further investigation to strengthen the latter findings.

### 2.6.2. Social evaluation in non-human species

Other than humans, the phenomenon has been studied only in non-human primate species, dogs and in cleaner-client reef fish interactions. In non-human animals, the ability to discriminate between prosocial and antisocial others was investigated from different perspectives, and researchers used different, but related terms to describe the phenomenon. In this overview, the conceptual approach of the original experimental studies provided the basis of the categorization. In the following, we use the terms negativity/positivity bias and social evaluation in the above meaning, and refer to the terms used in the original studies only in the subtitles.

#### Reputation formation in non-human apes

Researchers tested chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus*), gorillas (*Gorilla gorilla*) and orang-utans (*Pongo pygmaeus*) in different food sharing situations (Russell et al. 2008; Subiaul et al. 2008; Herrmann et al. 2013). In these studies, researchers used similar procedures in which subjects observed a human (or a conspecific) begging for food from two persons. In all cases, the prosocial partner gave food to the recipient (beggar), but the other partner either refused to share (Russell et al. 2008; Subiaul et al. 2008) or prevented the prosocial human to give food to the recipient (Herrmann et al. 2013). After the observation phase, subjects were allowed to choose between the partners who offered food to them. Upon subject's request, either the prosocial partner gave and the antisocial partner refused to give food (Subiaul et al. 2008) or neither of the partners shared food (Russell et al. 2008; Herrmann et al. 2013).

There are two experiments (Russell et al. 2008; Subiaul et al. 2008 Experiment 1) that are mostly comparable with the studies conducted with human infants. In Russell et al. (2008) chimpanzees observed a third-party interaction between three humans. They found that only chimpanzees, but not bonobos, orang-utans and gorillas prefer the prosocial human over the antisocial partner, after observing a food sharing situation between them and a human recipient. Unfortunately, in Russell et al. (2008) there is no information about the results of the critical first trial (whether there is a significant difference between times spent next to the two partners). However, subjects had direct experience with the partners during this trial which could influence their behaviour toward the humans later. Considering that in chimpanzees there was a decline in time spent next to the antisocial partner over the trials, it would be interesting to see whether there was a significant difference between times spent next to the two partners in

the first trial. Furthermore, because the antisocial partner did not simply refuse to give, but also hit the recipient when he tried to reach the container, subjects might have been simply afraid of the antisocial human and this is why they avoided her. Considering that there is a decline over trials in approaching the antisocial partner, but there is no increase in the case of the prosocial partner, we can conclude that chimpanzees might show negativity, but not positivity bias in this context.

Subiaul et al. (2008) tested the same chimpanzee subjects in three experiments relying on the same procedures. In the first experiment, in which two unfamiliar humans behaved prosocially or antisocially toward a familiar human, none of the chimpanzees showed any preference toward the prosocial human partners after 16 trials. Thus, in the second experiment subjects received an extensive training to choose the prosocial partner after direct interaction. They were tested in blocks of eight trials and reached the criterion when they chose the familiar prosocial human at least seven times out of eight in two consecutive blocks. Four chimpanzees (out of seven) who reached the criteria showed significant preference toward both prosocial familiar and unfamiliar humans in subsequent tests. In the third experiment, the same four subjects observed eight pairs of unfamiliar human partners interacting with another chimpanzee (six trials with each pairs of partners; third-party interaction). Subjects were tested in six trials with each pairs of partners and if they chose the prosocial one they obtained food from them (were reinforced for the correct choice), but not if they chose the antisocial partner. In the first test trials with the different partners, the mean preference toward the prosocial unfamiliar human was 53%. However, in case of three out of four subjects during the first four sessions (24 trials with four different pairs of partners) the choice of the prosocial partner increased to 75%. Thus it seems that chimpanzees in Subiaul et al. (2008) discriminated between prosocial and antisocial human partners only after receiving specific training. Furthermore, in the third experiment, subjects not only could rely on their earlier direct experiences with partners showing similar behaviour, but also during testing they received reinforcement to choose the prosocial partner (direct interaction). Thus it seems that chimpanzees do not show spontaneous discrimination between prosocial and antisocial human partners after indirect experience.

In their first experiment, Herrmann et al. (2013) exposed subjects (non-human apes and 30-months-old human children) to a prosocial partner who attempted to offer them a piece of food, when the antisocial partner interfered and prevented the action by taking the food away (direct experience). After directly interacting with the partners, orang-utans and human children (see earlier) chose the prosocial partner more often, but not chimpanzees and bonobos. In the next experiment, the same subjects observed the same partners behaving the same way toward

a third human (third-party interaction). In the test phase, both partners offered a piece of food to the subjects, but when they reached for it, both of the partners withdrew their hands. In this case orang-utans and chimpanzees, but not bonobos and human children, preferred the prosocial partner. It should be noted that some elements of the procedure used by Herrmann et al. (2013) could influence subjects' choice. For example, as a response to the stealing by the antisocial partner the prosocial partner expressed her frustration by hitting and pushing the antisocial partner. This behaviour of the prosocial partner could have elicited avoidance behaviour on the part of the subject, thus the nature of this partner was not necessarily considered as prosocial.

In most of these experiments, subjects engaged in direct interaction with the partners before the third-party interaction, thus we cannot separate the effect of this experience from their behaviour in the indirect context. Based on these, it is still unclear whether chimpanzees and orang-utans discriminate spontaneously between a prosocial and an antisocial partner, after witnessing third-party interaction. Further problem is that only prosocial and antisocial partners were presented to the subjects. Thus even evidence for discrimination between the partners would not fulfil our definition of social evaluation.

A recent paper investigated social evaluation in bonobos which resulted in interesting findings (Krupenye and Hare 2018). In their first experiment, Krupenye et al. (2018) applied the 'hill-paradigm' used in human infants earlier, with geometric figures as partners (e.g. Hamlin et al. 2007). In their second and third experiments, they used a similar procedure as Herrmann et al. (2013) played by unfamiliar human partners, in which the antisocial partner hindered the prosocial to give back a dropped toy to the recipient; in the test phase they both offered food to the subject. Authors found that bonobos preferred antisocial individuals over the prosocial ones across experiments, which is the opposite as expected in case of social evaluation, or in the presence of any of its building blocks. However, their fourth experiment revealed that bonobos' choice is probably the result of dominance rank of individuals based on the third-party interaction, rather than their level of prosociality. This is in line with observations that bonobos regularly beg to higher-ranking individuals in their natural habitat, to test their tolerance (Yamamoto 2015). Human toddlers also prefer dominant individuals; importantly however, they discriminate between winning when the losing partner defers, or winning by force (preferring the dominant individual in the former, but not in the latter scenario; Thomas et al. 2018). Thus it is an interesting question whether the dominance hypothesis found to be true in bonobos, can be a possible explanation (at least at younger age) in humans as well.

**Social evaluation in capuchin and marmoset monkeys**

In capuchin monkeys, Anderson et al. (2013) used a problem solving situation to investigate social evaluation. Capuchins could witness two human partners who sat next to each other. One of them was always the recipient who tried to open a container to obtain an object from inside. In different trials (within subject design) the other person helped, refused to help, tried to help, but failed, or simply failed to acknowledge the help requested by the other person. After having observed the interaction between two partners, the capuchins could choose from whom they accept a piece of food. The recipient served as a neutral partner considering that she did not behave prosocially or antisocially. The capuchins chose the neutral partner over the antisocial partner in all cases, however, they did not show preference toward any of the humans when the partner helped, tried to help or was occupied during the request (was prosocial or neutral). These results suggest that capuchin monkeys show negativity, but not positivity bias that is not considered as social evaluation according to our criterion. This result is similar to that of 3-month-old infants who also showed negativity, but not positivity bias after observing a helping interaction between inanimate agents (Hamlin et al. 2010). However, we should note, that this refers to the mean performance reported after repeated experimental trials, and we also have no information about capuchins' choice in the first trial.

In a different study, Anderson et al. (2013b) investigated whether capuchins discriminate between two humans after observing a third-party reciprocity situation. Subjects observed a ball-transfer between two humans; *A* requested balls and *B* gave her own, and later *B* asked them back. In this case, *A* either reciprocated or refused it by turning her head away. Then the partners offered food for the subjects who were allowed to choose from which of the partners they accept it. Capuchins did not show preference toward either of the partners after witnessing a reciprocated action by *A*; however, they chose the prosocial partner over the antisocial human after the non-reciprocated interaction. We suggest that in contrast to Anderson et al. (2013a), the recipient in this case was not a neutral agent considering that at the beginning of the interaction *B* transferred balls to *A*, thus it behaved prosocially. Based on this, capuchins observed an interaction between two prosocial partners, and between a prosocial and an antisocial partner. Thus the avoidance of the antisocial partner in the second scenario was not necessarily due to negativity bias, and we cannot exclude the possibility of the presence of positivity bias either.

Kawai et al. (2014) investigated sensitivity to third-party reciprocity in common marmosets (*Callithrix jacchus*). Similarly as in Anderson et al. (2013b), in case of the reciprocal event the two humans (*A* and *B*) exchanged food, while in the non-reciprocal condition there was an

initial transfer from *B* to *A*, but *A* refused to give food to *B*. Their results were similar as with capuchin monkeys (Anderson et al. 2013b), subjects were willing to accept food from both partner in the reciprocity condition, but they preferred partner *B* in the condition where *A* refused to transfer. However, because of the similarities in the procedures the same problem arises here as well, meaning that no neutral partner was introduced to the subjects, and thus discrimination between partners could be due to negativity and positivity bias as well.

Thus it seems that in capuchin monkeys at least negativity bias can be detected; however, we do not have convincing data on whether they show positivity bias as well, thus whether they are able to evaluate others socially. In case of marmoset monkeys, we are also lack of information about the presence of negativity and/or positivity bias.

### Social eavesdropping in domestic dogs

Recent findings suggest that dogs are able to coordinate their actions with each other and humans in cooperative tasks (Bräuer et al. 2013; Ostojić and Clayton 2014). Many dogs live in multi-human/dog groups, and get often in contact with unfamiliar people. Thus considering that humans provide them different resources, it would be advantageous to be able to obtain information by observing their interactions with others; showing avoidance of antisocial partners and/or preference toward prosocial ones. Domestic dogs were tested in food sharing situations to find out whether they show different behaviour toward two human partners based on their behaviour toward a third-party (Marshall-Pescini et al. 2011; Nitzschner et al. 2014; see below in detail). There has been only one study in which dogs were tested in a helping situation (Chijiiwa et al. 2015; see below in detail).

Marshall-Pescini et al. (2011), Freidin et al. (2013), and Nitzschner et al. (2014) used a similar food sharing situation as described for non-human primates. Although the results of the experiment by Marshall-Pescini et al. (2011) showed that dogs prefer the prosocial human partner over the antisocial partner, the latter two studies suggested that dogs' choice was influenced by the location of the human (in the test situation) rather than the identity and behaviour. Kundey et al. (2011) tested dogs in a similar third-party interaction. However, they varied several elements of the procedure, for example, in one experiment either the recipient was an inanimate self-propelled object or the human partners sat inside boxes (they were invisible). The unfamiliar prosocial partner gave food to the recipient by placing it in front of her, while the antisocial partner put it in front of the recipient, and when she reached for it, the partner removed the food (prevented the recipient to take it). They found that dogs reliably choose the prosocial partner across experiments over the antisocial one, thus suggested that they

are able to evaluate others based on their behaviour in a social context. Considering that dogs showed this choice even when the "partners" were two boxes or the human partners behaved toward an inanimate object, dogs might simply associate the exchange of food with one of the partners and did not evaluate them based on their behaviour toward another.

Nitzschner et al. (2014) conducted a study presenting a different situation than sharing food. Dogs observed an interaction between two human partners and a dog; the partner was either a nice human who behaved friendly with the demonstrator dog or a human who simply ignored the dog. Even though after direct interaction subjects spend more time next to the nice experimenter, after the third-party interaction dogs did not show different behaviour toward them. We suggest one alternative explanation other than raised in the original paper that can explain dogs' behaviour in this latter case. From the viewpoint of the demonstrator dog the humans could be considered as nice or ignoring; however, the subjects (witnessing the human-demonstrator interaction) were ignored by both humans (direct experience). We suggest that this direct experience could have greater effect on dogs than the information gathered in the third-party interaction.

Recently Carballo et al. (2015) investigated further whether dogs are able to discriminate between prosocial and antisocial humans after direct experience. The humans pointed at one of two bowls in front of the dog that contained food. However, while the prosocial partner let the dog eat the food, the antisocial partner took the food and ate it as soon as the dog found it. When there was a gender difference between the partners, dogs discriminated between them after six trials; 12 trials were needed for similar performance when both partners had the same gender (females). Thus it seems that even in case of direct interaction dogs need more experience with human partners to discriminate between them based on their behaviour.

Chijiiwa et al. (2015) implemented a helping scenario similar to the one used by Anderson et al. (2013a). Dogs observed that their owner tried to open a container, but failed and requested help from one of the two human partners who (depending on the experimental group) either helped (prosocial) or refused to help by turning her head away (antisocial). The other (neutral) partner sat there quietly without engaging in any interaction. In a control group the owner stopped manipulating the object and then one of the human partners turned her head away. Thus only one of the partners was active during the demonstration and the owner interacted with this partner only (no interaction in the control condition). In the test trials, dogs in the control group chose randomly. Dogs did not show any preference for the prosocial vs. neutral (non-active) partner. In contrast, dogs avoided the antisocial partner in favour of the neutral one. However, several aspects of the procedure could have influenced the results of Chijiiwa et al. (2015). In

case of Anderson et al. (2013a), the neutral partner was the recipient, thus subjects could see the action of the neutral partner as well, while here the neutral partner did not show any behaviour during the observation phase (no interaction with the recipient). Thus the only available information about this partner was that she offered food during the test trials (prosocial act in direct interaction with the subject). Also, in the four test trials, dogs had direct interaction with the partners who gave food to them upon request (including the neutral and antisocial partner). Thus information about the partners obtained during observations and in test trials were contradictory for some partners, and may have influenced the results. Importantly, recalculations of the original data showed no significant difference between conditions in the first test trial[1], i.e., no difference in subjects' choice between the 'active' (prosocial, antisocial, and control) and the neutral partners. It is also worth to mention that in this study the recipient was the subject's owner, thus the recipient/owner could carry over some contextual information from everyday life (interactions between the owner and others) to the situation used in the study.

In sum, although several studies were conducted with dogs, it is not clear whether they adjust their behaviour toward the partners based on partners' behaviour toward others in a third-party interaction. Furthermore, due to the procedural arrangements, we do not have clear information about the emergence of social evaluation or its components.

### Reputation formation in cleaner-client reef fish interactions

The formerly described species are either share the same evolutionary clade with humans (non-human primates) or live in close contact with them (dogs). However, we suggest that similar capacity might be shown in non-mammalian species as well. Bshary (2002) and Bshary and Grutter (2006) conducted studies on bluestreak cleaner wrasses and their client reef fish species. Cleaners remove the ectoparasites from their client fish, but some of them may consume the mucus and thus become a parasite instead of a cooperator. Clients also have the opportunity to eat the cleaner fish; however, this is less likely (Bshary 2002). Thus for the client it is crucial to predict the prosocial or antisocial nature of the unfamiliar cleaner fish. In their study Bshary and Grutter (2006) used a procedurally similar method to that used in primates and dogs. They found that clients spend significantly more time next to a cleaner that they had the chance to observe while cooperating, than next to a cleaner that did not engage in an

[1] Although the results of the first test trial (in which dogs only had indirect information about the partners) was not reported in the original study, by using the data reported in the Appendix of Chijiiwa et al. (2015) (Table 1) we found that there was no significant difference in any of the conditions (Binomial GLMM; condition × trial: $p = 0.870$; trial 1 in case of Helper condition vs. Non-helper condition: $p = 0.5$; Helper condition vs. Control condition: $p = 0.5$; Non-helper condition vs. Control condition: $p = 1.0$).

interaction with the model client fish. In this case, the second partner can be considered as a neutral partner and the cooperative cleaner as a prosocial individual, thus the choice behaviour of the clients can refer to a positivity bias. However, in this case choosing an 'unknown' partner who might be antisocial has high cost. Thus clients might simply avoid the potential antisocial partner, the potential harmful consequences. The results of Tebbich et al. (2002) strengthen this assumption. They found that during the first two minutes of an experiment cleaner fish spend more time in the proximity of a familiar than an unfamiliar client (*Ctenochaetus striatus*). In the field, Bshary (2002) also found that clients were more likely to choose (invite for inspection) the cleaner whose previous interaction was positive than the one that was chased off by the client or its client darted off (negative interaction). However, if there was a longer time lag (> 5 s), clients' choice was not affected by the previous interaction of the cleaner. Unfortunately, in this situation the client could choose only between prosocial and antisocial partners, thus it is not possible to establish whether the skills of these fish fulfil the criteria of social evaluation. It would be interesting to examine the behaviour of the clients when presenting them an interaction between a prosocial, antisocial, and 'unknown' partner in different arrangements to see whether we can detect negativity and/or positivity bias.

These results suggest that although currently the phenomenon is mainly studied in primates and dogs, it would be interesting and useful to conduct similar studies on other taxa as well.

### 2.6.3. Comparison of studies between non-human and human animals

#### The functional concept of social evaluation

The investigation of social evaluation from an evolutionary and comparative perspective indicates that there is a need for general agreement on terminology and definition. We put forward that the concept of social evaluation should be reserved for assigning partnership values to other individuals in the group independent from its direction (negative or positive), although it is clear that avoiding others in such context is a more prevalent skill in animals. Accordingly, social evaluation allows the individual to enhance its fitness by being able to choose its partners for cooperative interaction based on direct or indirect (third-party) experience. This functional definition seems to provide a general framework for comparing different clades of animals that depending on the evolutionary history and ecological status may or may not display this skill. Unfortunately, the possibilities of comparative investigations are limited, but from an ecological and phylogenetic viewpoint non-human apes could provide an opportunity to

establish specific hypotheses in relation to the manifestation of social evaluation. The few surviving species live in a variety of social organizations in which the significance of social evaluation could be different. Chimpanzees and bonobos live in large complex groups in which individuals engage in cooperative and competitive interactions, develop friendships (Silk 2002, 2003) and also form coalitions (de Waal 1984). In contrast, the hierarchical groups in gorillas typically consist of a female harem and their offspring led by an adult dominant male (Robbins et al. 2004). Finally, orang-utans are solitary for most of their life; many females live alone or with their offspring on non-overlapping territories of males (Singleton and Van Schaik 2002).

Thus based purely on their ecology we may predict that a well-developed ability of social evaluation should contribute to higher fitness in chimpanzees and bonobos, while its role in gorillas and orang-utans could be negligible. Alternatively, fully functional social evaluation may have evolved much earlier in primate evolution, and its manifestation depends on epigenetic factors (Chapman and Rothman 2009). In this case, testing captive individuals of these species may not provide meaningful insights because the social structure of these groups may differ from that in nature (Brent 1992; Boesch 2007), and their socialization to humans may also influence the development of social evaluation.

### Contradictory results and methodological issues

Researchers conducted similar studies with non-human primates and dogs both from the viewpoint of partners and situation (Russell et al. 2008; Marshall-Pescini et al. 2011); however, the results were contradictory in most of the cases. For example, in chimpanzees Russell et al. (2008) found that they show preference toward the prosocial human partner over the antisocial one after observing third-party interaction, but the results of Subiaul et al. (2008) suggest that even in direct interaction it takes several trials for chimpanzees to choose the prosocial partner. In contrast, in Herrmann et al. (2013) chimpanzees did not discriminate between the partners in a direct interaction, only after observing their behaviour toward another human later (indirect interaction).

It is also interesting that human infants' performance seems to be influenced by the method used. In case of human infants and toddlers, the set up that was used most often included inanimate objects as partners, and different helping situations were demonstrated to the subjects (Hamlin et al. 2007; Hamlin and Wynn 2011). Despite some differences in details (e.g. context-dependency), the results show that social evaluation emerges relatively early in humans, at around 5–6 months of age. However, when human adults were used as partners, even in a similar situation, researchers failed to find discrimination between the partners in 17- and

22-month-old toddlers (Dahl et al. 2013); they only found discrimination between the prosocial and antisocial human partners in 26-month-old toddlers. Herrmann et al. (2013) also failed to show discrimination between human partners in 30-month-old toddlers in third-party interaction using sharing situation. Thus it is likely that the different procedures measure different aspects of social evaluation in human children, and this should be clarified before these data are compared to those obtained from non-human animals.

There have been only two studies in which helping situation was used in non-human primates. Anderson et al. ( 2013a) found evidence for negativity bias in capuchin monkeys, and the findings of another study by Anderson et al. (2013b) also suggests that capuchin monkeys show negativity and/or positivity bias after observing the interaction between two human partners. In bonobos however, the same helping situation as used in human infants failed to measure social evaluation in subjects (Krupenye and Hare 2018), calling attention on carefulness in interpreting comparative data, as superficial similarity between experimental setups may fail to reach functional similarity as expected.

An important issue should be considered here as well: helping and sharing are two distinct domains (Warneken and Tomasello 2009), and the presence of one does not indicate the functioning of the other. For example, it has been found that both human children and chimpanzees show helping behaviour, but only the former tend to share resources with others (for a review, see Warneken and Tomasello 2009). In light of this, we suggest that it is unfortunate that helping has been used most often in children, but sharing situations in case of non-human species when investigating social evaluation. Thus, we propose that in future studies this issue should be taken into account as well.

One might argue that in non-human primates and dogs using heterospecific partners could affect the outcome. However, companion dogs spend their life with humans and the tested non-human primates were also socialized to humans. Due to their extensive experience with humans it was not necessarily disadvantageous to use humans as partners in these studies but further comparative studies are warranted. However, former experiences with conspecifics and/or humans, and subjects' expectation toward them can influence subjects' behaviour in studies investigating social behaviour and cognition (Krause et al. 2011; Gergely et al. 2015). Several studies with domestic dogs support this assumption (Szetei et al. 2003; Erdőhegyi et al. 2007; and see also Topál et al. 2009) in which researchers showed that some aspect of dogs' cognitive skills can be masked by using human social communicative cues and thus false conclusions can be drawn about their cognitive abilities. Utilization of unfamiliar moving inanimate objects (robots) as social partners can be useful in such investigations, especially if

the physical appearance of the robot does not resemble the embodiment of the subject species or any heterospecifics with whom they engage in daily interactions (e.g. Abdai et al. 2015; Gergely et al. 2015; Petró et al. 2016). This way the test itself can be controlled by the experimenter more efficiently, and it is also less likely that the robotic partner induces aversion. The novelty of the social partner hinders the possibility that subjects have any preliminary assumption about how the partner should behave in a given context (separation of expectations and the displayed behaviour). The results of studies conducted with human infants using unfamiliar inanimate objects (Hamlin et al. 2011) and humans (Dahl et al. 2013) as partners also suggest that utilization of robots in such investigations can be advantageous.

Although, in the present review our main concern was about the emergence of social evaluation in third-party interactions, we would like to emphasize that subjects' direct experience is also important (see above). Unfortunately, to our knowledge no studies have been conducted in which researchers would have systematically tested and compared the role of direct and indirect experiences in this context. To investigate such questions, experimenters would need to control subjects' experiences with other individuals (either conspecifics or heterospecifics). The utilization of unfamiliar inanimate agents may provide a solution to this problem because this offers the possibility to control subjects' social experience. This way the amount of familiarization with the potential social partners can be manipulated systematically. Only such well-controlled methods can provide us information about the cues and triggers of the social evaluation system.

## 2.7. Revisiting development and evolution in light of current literature

Although in non-human species, data about the presence of social evaluation is missing, in humans we have information about its potential development (Figure 2.1). Based on a series of studies conducted by Hamlin and colleagues, it seems that at three months of age only negativity bias is present in human infants (Hamlin et al. 2010), and positivity bias develops only later, between the age of three and six months (Hamlin et al. 2007). Further results suggest that at around five months of age infants may only rely on the outcome of the actions performed by others and not on the valence of their actions (Hamlin 2013b; but see Hamlin 2014 for opposing results). However, infants at the age of eight months do not only discriminate between others based on their behaviour, regardless of the outcome of their actions, but are also able to take

into consideration the partnership value of the recipient of the behaviour as well, and calculate relative partnership values (antisocial behaviour toward an antisocial agent/recipient results in positive partnership value). Based on the results of Skowronski & Carlston (1987), adult humans are also able to weigh the behaviour of others based on their importance and/or reliability. Thus in specific situations some behaviour counts as a better predictor of the individual's future behaviour than others, and partnership values can differ based on this (e.g. extremely vs. moderate antisocial behaviour). However, we do not have information about when this factor develops.

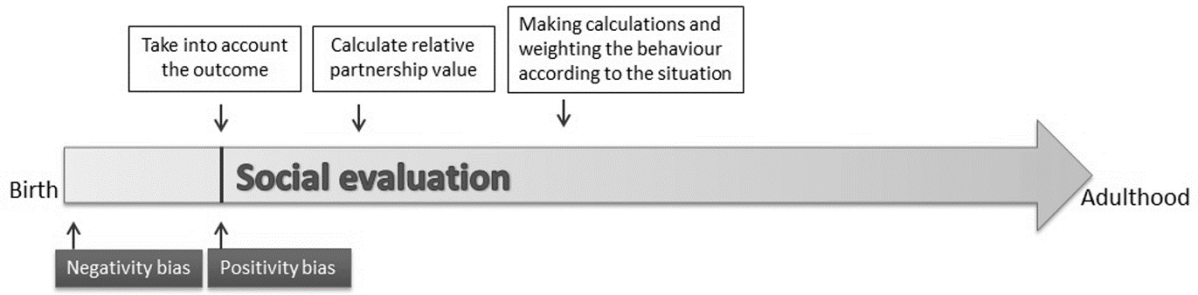


**Figure 2.1.** Development of fully fledged social evaluation in humans. Negativity bias seems to emerge soon after birth (Hamlin et al. 2010), and at around 6 months of age positivity bias also manifests (Hamlin et al. 2007). According to Hamlin et al. (2011), at first infants consider only the outcome of actions, but later they are able to take into account the context as well. Skowronski & Carlston (1987) showed that at least adults weigh the performed behaviour of others.

Based on current literature, it seems that similar phenomena can be detected in different taxa and we cannot exclude the common evolutionary origin. However, methodological differences disallow to draw strong conclusions (see details below). Anderson and colleagues (2013a) suggested that social evaluation (according to our criteria only negativity bias) in third-party interactions dates back to the common ancestor of Old World and New World monkeys; however, they do not exclude the possibility that similar phenomena in human infants and capuchin monkeys are the result of convergent evolution. Due to its significance for survival, we suggest that negativity bias may have evolved earlier on the evolutionary scale, and it is widespread among animals. We further suggest that negativity and positivity bias may emerge independently not only developmentally, but they may have different origins from an evolutionary point of view as well.

### 2.7.1. Analogies on the evolutionary and ontogenetic scales

The emergence of social evaluation can be presented on a timeline that may be analogous on evolutionary and ontogenetic timescales (Figure 2.1). Although in non-human animals there is lack of data on the emergence of social evaluation, results in human infants shows that negativity bias develops relatively early which is followed by the manifestation of positivity bias (Hamlin et al. 2010; Hamlin 2014). Based on the ecological significance (larger effect on survival) and a single study in capuchin monkeys (Anderson et al. 2013a) which used a comparable method to that applied in human infants (Hamlin and Wynn 2011), we predict that negativity bias may be more widespread among non-human animals, and also evolved earlier. However, recent evidence in bonobos suggest that this may not be the case.

## 2.8. Modelling the mechanism of social evaluation

Most experimental studies have been aimed at showing the presence or absence of social evaluation at a certain age (in humans) or in non-human animal species. Little attention has been devoted to mechanisms. Further methodological problem is that in infants spontaneous testing of social evaluation was preferred, while in non-human animals more or less training was applied before testing for social evaluation.

We have suggested that individuals may assign different partnership values to others based on obtaining evidence by either direct or indirect interactions. At some point later in ontogeny, they may form specific categories for ‘preferred/prosocial’ and ‘non-preferred/antisocial’ individuals with whom they have extensive experience. Unfortunately, most experimental setups test only for short term social evaluation in which the subject is exposed to a single scenario with unfamiliar partners. However, there is some experimental evidence that infants are also able to calculate relative partnership values when they prefer the antisocially behaving (basically prosocial) partner if it punishes an antisocial partner (Hamlin et al. 2011). Some authors further suggested that individuals might be able to weight the actions of the partners based on their importance and/or reliability as well. Thus some behaviour, depending on the situation it was performed in, can count as a better predictor of the individual’s traits than others (Skowronski and Carlston 1987). For example, Skowronski and Carlston (1987) found that adult humans rely more on negative behaviour in case of morality related context, and that extremely negative behaviour receives more weight than moderate negative behaviour.

Based on this, we have developed a simple descriptive model for social evaluation which may provide a common ground for comparative experiments (Figure 2.2). In this model, individuals assign negative or positive values to the behaviours performed by other individuals in direct or indirect interactions. Novel information about their behaviour shapes the mental representation of them. Social evaluation manifests in the individual's choice of the neutral or the prosocial partner depending on the available partners, and whether both positivity and negativity bias can be detected or only one of them is present (for example, if only negativity bias is present, the individual do not choose between a neutral and a prosocial partner). Considering that the outcome of an interaction itself is not necessarily the best predictor of the future behaviour of others, some species may also be able to take into account the context as well (e.g. negative behaviour can have positive value based on the context it was performed, see (Hamlin et al. 2011).

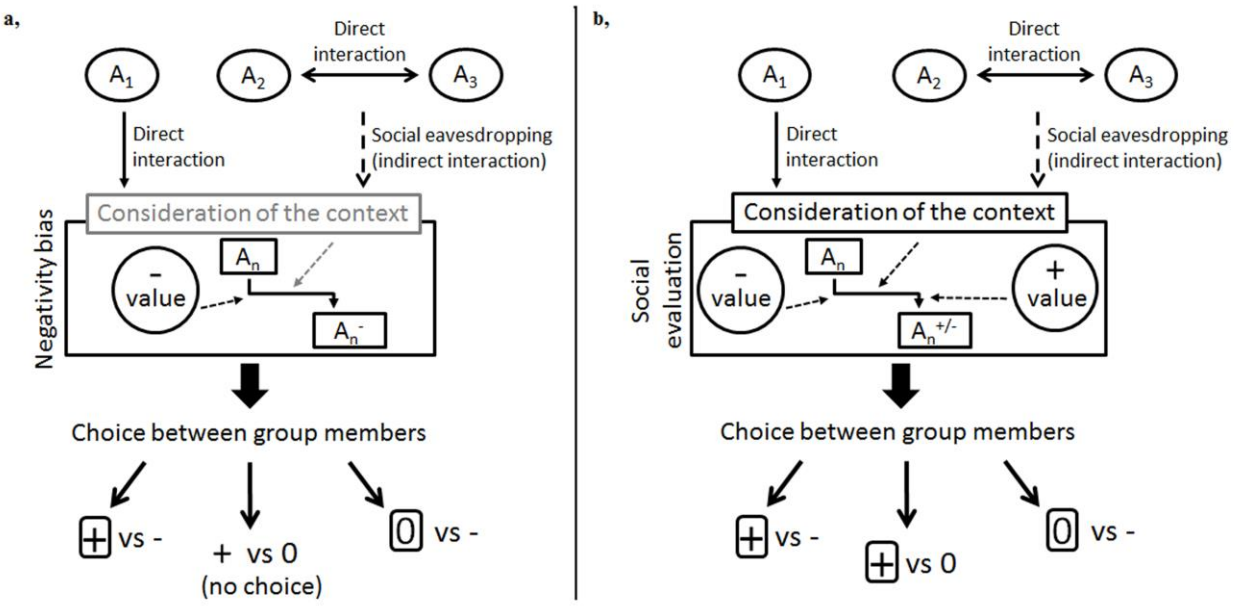


**Figure 2.2.** Two models of negativity and positivity bias, and the emergence of social evaluation. (a) This model is based on Anderson et al.'s (2013a) results in capuchin monkeys; contextual evaluation is only hypothetical, there is no evidence in the study. (b) Simple model of social evaluation based on studies by Hamlin et al. (2007) in human infants from around 6 months of age. $A_n$ stands for the members of the individual's group. The social evaluation system of the individual cumulates the negative and positive values that are assigned to specific behaviour of $A_n$ in a given context. The individual chooses between the group members based on their overall partnership value.

## 2.9. Conclusion

Here, we defined social evaluation as the integrated behaviour and cognitive system of negativity and positivity bias, and proposed that evaluation based on negative or positive aspects of behaviour may have different evolutionary and ontogenetic origins. We further suggest that discrimination between prosocial and antisocial partners in cooperative context is likely to be widespread among species living in long-term closed social groups. Results of studies conducted with non-human mammals and observing interactions among client and cleaner reef fish suggest that negativity and/or positivity bias can be detected in species other than humans. However, we have no clear evidence whether non-human animals are able to show such preference only upon spontaneous observation of third-party interaction.

By conducting studies with a wider range of species having different phylogenetic and ecological backgrounds, we could obtain important information about the origin and development of social evaluation. Considering that in humans social evaluation is discussed in relation to morality, it would be important to find out more details about the relative contribution of genetic and environmental factors to this capacity.

# 3. THIRD-PARTY INTERACTIONS: A STUDY OF JEALOUS BEHAVIOUR

Jealous behaviour emerges when an important social relationship with a valued social partner is threatened by a third-party, a rival individual (e.g. Parrot and Smith 1993; Mize and Jones 2012; Hart 2016). Accordingly, an individual displays jealous behaviour if he tries to direct the attention of the valued social partner to itself and attempts to interrupt the interaction between the valued social partner and the social rival in different ways (e.g. pushing, attacking, agonistic displays). Regarding that social relationships can be crucial for survival (parent-offspring relationship) and fitness (romantic/sexual relationship), behaviours that facilitate to maintain these relationships are adaptive. Thus we assume that jealous behaviour emerges in a wide range of animal species despite it has been described almost exclusively in humans (but see e.g. Morris et al. 2008; Harris and Prouvost 2014; Prato-Previde et al. 2018).

Primary emotions are thought to be innate and present in both human and non-human animals, whereas secondary emotions are assumed to arise from complex cognitive processes, and acquired during development (Ekman 1992a, b; Becker-Asano and Wachsmuth 2010; Panksepp 2011; Panksepp and Watt 2011). Jealous behaviour is thought to be controlled by a secondary emotion ('jealousy') (e.g. Bauminger 2013; Panksepp 2013; but see Buss et al. 1992; Draghi-Lorenz et al. 2001 who argued that jealousy may be a primary emotion) and it is highly debated whether (1) it is present in non-human species and (2) the emotional state underlying this behaviour is comparable to that in humans (Morris et al. 2008). It has been assumed that children younger than two years of age do not show jealous behaviour because it requires complex sociocognitive skills (Case et al. 1988; Draghi-Lorenz et al. 2001; Hart 2016) and they lack the underlying emotional state; however, recent findings suggest that infants from six months of age already display jealous behaviour (Hart and Carrington 2002). Draghi-Lorenz et al. (2001) critically reviewed the most important theories about the underlying mental mechanisms that may be required for the appearance of secondary emotions. They concluded that despite the previous views, the presence of secondary emotions may not require interpersonal awareness, and that rudimentary forms of these emotions may be present at early development (see also Hart 2016). We suggest that similar theoretical framework as introduced for human infants may apply to non-human species as well. Alternatively, jealousy may not emerge as a distinct emotional state but a blended emotion, i.e. it is the result of an interaction between primary emotions (anger, sadness and may fear) (Parrot and Smith 1993; Harmon-

Jones et al. 2009; Hart 2016). This could enable the emergence of jealousy in non-human species, considering that primary emotions are probably present in a wide range of mammalian species (e.g. Plutchik 2001; Panksepp 2011; see also Buss 2014).

Recent research shows that infants younger than one year display jealous behaviour when the mother focuses her attention to a social test partner, a realistic looking doll in most studies (e.g. Hart et al. 1998, 2004; Hart and Carrington 2002; Mize and Jones 2012; Mize et al. 2014; but see e.g. Masciuch and Kienapple 1993; Bauminger et al. 2008 who used children as social test partners). Across studies researchers have suggested that infants and toddlers display behaviour and facial expressions that may be manifestations of jealousy (Hart et al. 1998, 2004; Hart and Carrington 2002; Mize and Jones 2012; Mize et al. 2014; for a review see Hart 2016). These behaviours include closer proximity to, more approach of, increased gaze toward, and more touch of the mother in the presence of a social test partner compared to a non-social test partner. Subjects also displayed more negative affect (angry and sad facial expressions) and lower level of joy. Importantly, subjects showed these behaviours and facial expressions more intensively when the mother was attentive to a social test partner, but not in case of a female stranger (Hart et al. 1998). Although in the original studies they referred to all the test partners as *rivals*, we prefer to use the more neutral *test partner* term, as we cannot be sure whether subjects (human infants and toddlers, and non-human species; see below) consider these agents as rivals *per se*.

There have been only a limited number of studies investigating jealous behaviour in non-human species (Cubicciotti and Mason 1978; Rilling et al. 2004; Harris and Prouvost 2014; Maninger et al. 2017; Cook et al. 2018; Prato-Previde et al. 2018b, a). In a questionnaire study by Morris et al. (2008) dog owners reported jealous behaviour in social triads, when the owner paid attention to a potential rival (they also collected information about secondary emotions in pet cats, horses, rodents and birds, but not in details; see also Konok et al. 2015), and recently Martens et al. (2016) found similar reports from dog owners. Harris & Prouvost (2014) conducted the first experimental study with dogs, in which they used three test partners: stuffed dog (social test partner); unfamiliar object and book (non-social test partners). Dogs looked longer at the test partner, touched/pushed more often the owner and test partner, and snapped more often the test partner during the stuffed dog condition compared to the non-social test partner conditions. They also found that subjects looked longer at the owner, whined more and tried to get between the owner and test partner more often in the presence of the stuffed dog compared to the book condition, but they did not find difference regarding the unfamiliar object. Based on these data it seems that dogs may show jealous behaviour, but overall dogs did not

display a clear distinction between the social and unfamiliar non-social test partners. Thus we caution to interpret these results as an evidence for jealous behaviour in dogs (see also Prato-Previde et al. 2018b). Although authors claimed that dogs accepted the stuffed dog as real because they sniffed its anal region and showed agonistic behaviour toward it, we suggest that dogs' behaviour could be due to distress elicited by the dog-like inanimate object or interest in it. Further, the stuffed dog barked, whined and wagged its tale which are used in communicative interactions; thus even if subjects considered the test partner as a real dog based on its behaviour and physical appearance, these communicative signals used inappropriately might reveal that the test partner is inanimate or make the situation artificial. Also, considering that the tests were carried out in the subjects' own home, dogs' behaviour might be considered as territorial aggression.

Three recent studies also aimed at investigating jealous behaviour (jealousy) in dogs. The results of Prato-Previde et al. (2018b) confirmed that using fake dog as potential rival does not elicit jealous behaviour in dogs, but their behaviour is more likely to be triggered by the artificialness of the test partner. Dogs' behaviour did not differ in case of fake dogs (social test partner) and a puppet (unfamiliar non-social test partner), and they displayed similar behaviour when a stranger attended to these objects, not only when the owner. Thus the behaviour was probably not due to a potential threat to their important relationship. Cook et al. (2018) attempted to investigate jealousy by applying brain imaging (fMRI) while dogs were watching their owner's behaviour live. They used a fake dog as potential social rival and the owner gave food to the test partners (fake dog and bucket). Considering the above studies, the findings of Cook et al. (2018) on the higher amygdala activation when the owner gave food to the fake dog (compared to putting it into a bucket) is not likely to be the result of the jealousy. Other than the method applied (fake dog as potential rival and the use of food), higher amygdala activation can be the result of other affective states as well (e.g. Zald 2003; Harmon-Jones and Harmon-Jones 2018; Abdai and Miklósi 2018). Further, jealous behaviour does not only include aggression toward the rival, but other (non-agonistic) behaviours as well (see above), thus measuring only one brain area can lead to false conclusions.

Prato-Previde et al. (2018a) also conducted an investigation using real dogs (another dog from the same household) as potential rival in jealousy-evoking situation. They found different behaviour in dogs when the owner attended to the other dog from the same household compared to when he/she was reading a newspaper, but *significant* difference in behaviour was only found in case of gazing at the owner. They also showed individual variation in behaviour and suggested that this might cause the lack of significant differences in their experiment.

Considering that this study was published long after our study was conducted, the results and design of this study could not be taken into account in our experimental setup.

Several alternative explanations have been raised to account for dogs' behaviour in such situations (if we consider claims that these can be defined as jealous behaviour) (e.g. Morris et al. 2008). Two specific suggestions concern territoriality (see above) and that the behaviour observed in these situations is the result of dog's rank in hierarchy (see dominance relationships in Bradshaw et al. 2009). One may expect that in multiple-dog households where dogs' relationship can be described by dominance, the dominant individual may interfere when (one of) the subordinate dog(s) engage in exclusive interaction with the owner, that we label as jealous behaviour. Other explanations include protectiveness, playfulness and boredom (Morris et al. 2008).

We propose that behaviour displayed by dogs when their relationship with their owner is threatened by a social rival, can be labelled as jealous behaviour. First, family dogs depend on their owners who provides them shelter, food and protection; thus maintaining this relationship can be crucial for survival. Second, it has been showed that dog-owner attachment is functionally similar to mother-filial attachment (e.g. Topál et al. 1998; for a review see Prato-Previde and Valsecchi 2014), thus we assume that the potential loss of relationship with the owner would elicit similar behaviour in dogs, to that in human infants and toddlers in similar situation. Thus dogs seem to be an interesting species to study jealous behaviour from a comparative point of view. We suggest that previous attempts failing to show jealous behaviour in dogs (see Prato-Previde et al. 2018b on the results of Harris and Prouvost 2014) can be the result of the method applied and do not exclude that jealous behaviour indeed emerges in dogs (see also Prato-Previde et al. 2018b).

## 3.1. Experimental investigation of jealous behaviour in dogs

Here we aimed to examine whether dogs show jealous behaviour when the owner gives attention solely to a social test partner. Compared to the previous studies (Harris and Prouvost 2014; Prato-Previde et al. 2018b; but see Prato-Previde et al. 2018a), we used real dogs as social test partners (familiar and unfamiliar) and tested dogs at an unfamiliar place (to exclude territorial aggression; see also Prato-Previde et al. 2018b, a). We further collected background information on our subjects regarding the households they live in, their jealousy-related behaviour and context in which it occurs, and about their rank in hierarchy in the household.

We hypothesised that jealous behaviour (e.g. owner-oriented behaviour (trying to direct the owner's attention); attempts to separate the owner and test partner) manifests only (mainly) in the presence of social test partners, i.e. in the presence of potential rivals. We further expected that subjects show more test partner-oriented behaviour toward the unfamiliar than the familiar social test partner. We hypothesised that dog's rank (dominant or subordinate) does not have an effect on their behaviour. Alternatively, the behaviour described as jealous behaviour should be displayed by dogs in the presence of all test partners if it is due to playfulness or boredom; but it should not be displayed in case of the familiar dog if it is due to protectiveness.

### 3.1.1. Method

#### Subjects

Ethical approval was obtained from the National Animal Experimentation Ethics Committee (PE/EA/3741-4/2016). Owners provided a written consent form to voluntarily permit their dogs to participate in the study.

We tested 25 dogs from multiple-dog households. We could not finish testing one dog because the dog showed distress in the room. Thus we had 24 dogs in the final analysis (11 different breeds and 14 mongrels; 14 females; mean age (year) ± SD 4.9 ± 2.71; see Table A1 in Appendix).

#### Questionnaire

Owners filled in an online jealousy questionnaire about the subject dogs prior to the test, the invitation of dogs depended on owners' report (see responses in the Supplementary Information). The invitation to the test depended on the following questions of the jealousy questionnaire: (1) How jealous do you think your dog is compare to the average dog? (scale from 1 to 10), (2) Who does the dog usually gets jealous of? (3) Where does your dog get jealous? (at home, at unfamiliar places; on a scale from 1 to 5). We only invited dogs the owner of which indicated that the dog shows jealous behaviour toward another dog in the household, and/or other dogs in general. Owners that filled in the questionnaire (overall 631 dogs) gave a mean (± SD) 5.68 (± 2.67) jealousy score to their dogs; a mean (± SD) 3.19 (± 1.43) score at home, and 2.36 (± 1.33) score at unfamiliar places. The tested dogs had a mean (± SD) 7.08 (± 1.81) jealousy score given by the owner; a mean (± SD) 4.04 (± 1.11) score at home, and 2.65 (± 1.34) score at unfamiliar places. In case of one subject the owner filled in the

questionnaire for the other dog in the household (i.e. we had information about the familiar dog (test partner), not the subject). Based on the data provided by the owner we could decide whether the subject dog was the dominant or subordinate one in the household (as information about one dog provides information about the other; see below), but we do not have the other information.

Our aim was to investigate whether we find evidence on the phenomenon in the species, thus we pre-selected subjects that according to the owner's report tend to show this behaviour. Pre-selection was necessary, because we suspected that if jealous behaviour emerges in dogs, there would be individual differences and some individuals (similarly as in case of humans) would not show jealous behaviour (see also Morris et al. 2008 in which jealousy was reported only in case of 81% of the dogs (N=337)).

In addition, we asked the owners four questions to decide whether the dog has a dominant or subordinate rank among dogs in the household (based on Pongrácz et al. 2008, 2012): (1) *When a stranger comes to the house, which dog starts to bark first (or if they start to bark together, which dog barks more or longer)?*, (2) *Which dog licks more often the other dog's mouth?*, (3) *If the dogs get food at the same time and at the same spot, which dog starts to eat first or eats the other dog's food?*, and (4) *If the dogs start to fight, which dog wins usually?*. We considered the dog dominant if the owner named the subject dog in the answer to the fourth question, or at least twice in the other three questions. We considered the dog as subordinate if the owner indicated another dog from the household in the fourth question, or at least twice in the other three questions. This is a slight change compared to the original criteria used by Pongrácz et al. (2008, 2012) who based the decision on the response to the fourth question, or when the owner uniformly indicated the same dog in response to the other three questions. Pongrácz et al. (2008, 2012) invited dogs based on owners' response to these questions, thus they could categorise the dogs as dominant or subordinate prior to the test. Considering that in the present study the effect of dominance rank among dogs on their behaviour was not the main question, we did not base the invitation on this. However, we suggest that this change in criteria does not weaken the argument (although these results should be treated with caution).

In case of 7 dogs the owner's response did not allow for determining whether the dog was a dominant or subordinate individual. In the case of one dog the social status was decided only on the basis of the first three questions because the owner claimed that the subject dog wins in fights only due to the size difference between the dogs (Sheltie vs. Belgian shepherd). In the analysis we had 11 dogs labelled as dominant and 6 labelled as subordinate.

## Test partners

We used four different types of test partners: familiar dog, unfamiliar dog, unfamiliar object and familiar object. The familiar dog was (one of) the other dog(s) from the household. The unfamiliar dog was a middle-sized, neutered female mongrel dog with therapy dog training. Before the test the subject dog and the unfamiliar dog were introduced to each other for about 5 min to see whether any of them shows distress in the presence of the other (in case the owners indicated distress in either the subject or the unfamiliar dog, the introduction was interrupted immediately). We could not test two dogs in the unfamiliar dog condition; however, we tested them in the all other trials. The owner of the unfamiliar dog stood in the room, next to the door she entered during the Unfamiliar dog condition. This allowed her to intervene if needed (e.g. dogs start to fight). She avoided any eye contact with the subject dog and did not talk during the trial.

The unfamiliar object was a remote control car (#32710 RTR Switch Abarth 500, 28 cm x 16 cm x 13 cm) that did not move during the trial. In case of dogs that have already seen the remote control car moving in previous studies (e.g. Abdai et al. 2015; Gergely et al. 2015; Petró et al. 2016), we used a thermos (25 cm x 14 cm x 14 cm) that had similar colour and size as the car. The familiar object was a newspaper. All subjects encountered all test partners (see above the exception).

## Procedure

Dogs were tested in a 5.2 m x 3 m test room at the Department of Ethology, Eötvös Loránd University. All tests were recorded by four cameras attached to the ceiling.

We had five trials separated by ca. 1-2 min breaks. All trials consisted of two phases: familiarization phase (30 s) and test phase (90 s) that followed each other without a pause. In Trial 1 and 5 the test partner was the familiar dog (condition Familiar dog I and Familiar dog II) to be able to examine the consistency of the behaviour of subjects and the effect of time spent in the room (e.g. fatigue). In Trial 2, 3 and 4 the test partners were the unfamiliar dog, unfamiliar object, and familiar object (conditions named accordingly); we counterbalanced the order of these among subjects.

In Trial 1, the owner and the two dogs entered the room. Dogs could explore the room while the Experimenter (E) informed the owner about the procedure. In the other trials, E placed the test partner objects in the room after the owner and subject entered. The subject dog and the unfamiliar dog entered the room at the same time. The familiarization phase started when E left

the room. During all familiarization phases the owner ignored both the subject and the test partner; he/she measured the 30 s on a stopwatch.

After the time elapsed, the test phase started during which the owner focused his/her attention on the test partner while continued to ignore the subject. In Trial 1, E told the owner to behave in a way that usually elicits jealousy in the subject dog. Owners mostly choose to pet and talk to the test partner. After Trial 1 ended, E told the owners to behave in the same way as with the familiar dog in Trial 1 in the following trials, in order to make the conditions as similar as possible (e.g. in case of the familiar object the owner should read aloud only, if he/she was talking to the familiar dog in Trial 1, and had to repeat at least the most often used words that he/she used before).

### Behavioural variables and data analyses

Tests were analysed with Solomon Coder 16.06.26. (developed by András Péter: http://solomoncoder.com). We excluded two dogs from the Unfamiliar dog condition (see above), and we could not code the behaviour of one dog in Trial 1 (Familiar dog I condition) because the owner's positioning blocked the view of the cameras to the subject.

We measured subjects' behaviour only in the test phase. Coded behavioural variables were: looking duration at the owner, test partner or owner-test partner interaction (s), duration of body positioned toward the owner, test partner or owner-test partner interaction (s), duration of touching the owner, test partner or owner-test partner interaction (s), duration of moving toward and in parallel with the owner or test partner (owner-, and test partner-related motion) (s), duration of moving toward the owner-test partner interaction (s), and time spent within 0.5 m of the owner. We also coded how many times the subjects tried to interrupt the owner-test partner interaction (move between them). Inter-coder reliability for all variables were tested on a random subsample of the recordings (Cristina Baño Terencio; 20 % of the subjects) (IBM SPSS 22, Cronbach's alpha; see results in parenthesis (mean ± SD)). For the statistical analysis we kept the looking duration (0.750 ± 0.124), duration of body position (0.719 ± 0.106), time spent next to the owner (0.884 ± 0.077), and attempts of interruption data (0.862 ± 0.087). However, we excluded the duration of touch (0.649 ± 0.148) and motion (0.592 ± 0.182) from the analysis due to the low alpha values.

We used IBM SPSS 22 for statistical analyses. Principal component analysis (PCA) with Varimax rotation, Eigenvalue > 1 was used for data reduction. We decided the number of factors (three) after the visual inspection of the Scree test. Factor scores were calculated by SPSS automatically, using Regression method.

We used Box-Cox transformation in PC I (Lambda = 0.5), PC II (Lambda = -0.2) and PC III (Lambda = -1.5) as well. We used linear GLMMs to analyse the effect of dominance rank, trial, condition and order of condition on the principal components. Backwards model selection was based on AIC values; the model with the lowest AIC value was kept, we considered a model better when delta AIC was ≥ 2. For significant explanatory variables in the final models, we provide contrast estimates (B ± SE) and t values. For non-significant variables we provide test statistics before exclusion from the model.

Frequency of attempts to interrupt the owner-test partner interaction was not normally distributed according to the visual inspection of the Q-Q plots and based on the Kolmogorov-Smirnov test (Kolmogorov-Smirnov test, Familiar dog I: $D_{22}$=0.156, p=0.172; Unfamiliar dog: $D_{22}$=0.249, p=0.001; Unfamiliar object: $D_{22}$=0.340, p<0.001; Familiar object: $D_{22}$=0.400, p<0.001; Familiar dog II: $D_{22}$=0.187, p=0.044). We used related-samples Friedman test to compare the frequency of interruption of the owner-test partner interaction between conditions. Pairwise comparison by SPSS relied on Dunn's pairwise post hoc tests followed by Bonferroni correction for multiple testing.

### 3.1.2. Results

All behavioural variables, but the interruption of interaction have been included in the principal component analysis (PCA). Items were grouped into three principal components that accounted for 78.4 % of the common variance. The principal components have been labelled as *Interaction-oriented Behaviour* (PC I), *Owner-oriented Behaviour* (PC II) and *Test Partner-oriented Behaviour* (PC III) (Table 3.1).

**Table 3.1.** Loadings of items, explained variance, and Eigenvalues of the three factors (PCA). Only loadings greater than 0.5 are shown.

| | **PC I –** ***Interaction-oriented Behaviour*** | **PC II –** ***Owner-oriented Behaviour*** | **PC III –** ***Test Partner-oriented Behaviour*** |
|---|---|---|---|
| **Body oriented toward the interacting parties** | .860 | - | - |
| **Looking at the interaction** | .806 | - | - |
| **Staying near the owner** | .685 | - | - |
| **Looking at the owner** | - | .885 | - |
| **Body oriented toward the owner** | - | .841 | - |
| **Body oriented toward the test partner** | - | - | .930 |
| **Looking at the test partner** | - | - | .924 |
| **Explained variance (%)** | 32.8 | 27.1 | 18.6 |
| **Eigenvalues** | 2.29 | 1.89 | 1.30 |

There was a significant difference among conditions regarding the *Interaction-oriented Behaviour* ($F_{4,112}$=5.053, p=0.001). Subjects showed less *Interaction-oriented Behaviour* in the Familiar object condition than in case of other test partners, except for the Unfamiliar dog condition (Table 3.2; Figure 3.1).

**Table 3.2.** Comparison of the emergence of *Interaction-oriented Behaviour* between conditions (linear GLMM; significant differences are indicated with bold letters). For significant explanatory variables in the final models, we provide contrast estimates (B ± SE) and t values. Familiar dog I stands for the first, Familiar dog II stands for the last trial. Direction of difference is *Columns* vs *Row*, i.e. behaviour was more/less emphasized in *Column* compared to *Row*.

| | | **Social test partners** | | **Non-social test partners** | |
|---|---|---|---|---|---|
| | | **Unfamiliar dog** | **Familiar dog II** | **Unfamiliar object** | **Familiar object** |
| **Social test partners** | **Familiar dog I** | p = 0.753 | p = 0.576 | p = 0.753 | **B±SE=0.457±0.168 $t_{112}$=2.791 p=0.048** |
| | **Unfamiliar dog** | - | p = 0.246 | p = 0.750 | p=0.246 |
| | **Familiar dog II** | - | - | p = 0.750 | **B±SE=0.690±0.162 $t_{112}$=4.267 p<0.001** |
| **Non-social test partners** | **Unfamiliar object** | - | - | - | **B±SE=0.520±0.162 $t_{112}$=3.213 p=0.015** |

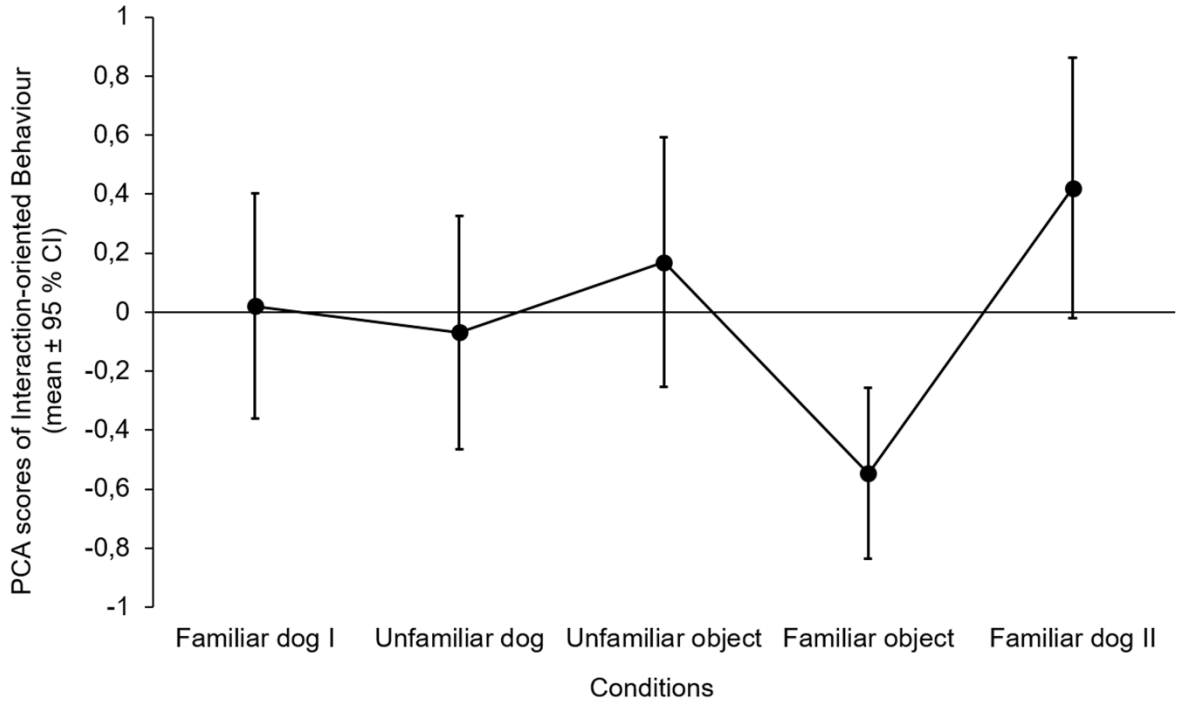


**Figure 3.1.** PCA scores of the *Interaction-oriented Behaviour* principal component in different conditions. Figure shows the original PCA scores before the Box-Cox transformation. The order of Unfamiliar dog, Unfamiliar and Familiar object conditions were counterbalanced among subjects.

Occurrence of *Owner-oriented Behaviour* also differed between conditions ($F_{4,112}$=6.453, p<0.001). There was no difference between the Familiar dog (I and II) and Unfamiliar dog conditions, but dogs showed more *Owner-oriented Behaviour* in the Familiar dog I condition than in case of the objects, and also in the Familiar dog II condition compared to the Unfamiliar object condition (Table 3.3; Figure 3.2).

**Table 3.3.** Comparison of the emergence of *Owner-oriented Behaviour* between conditions (linear GLMM; significant differences are indicated with bold letters). For significant explanatory variables in the final models, we provide contrast estimates (B ± SE) and t values. Familiar dog I stands for the first, Familiar dog II stands for the last trial. Direction of difference is *Columns* vs *Row*, i.e. behaviour was more/less emphasized in *Column* compared to *Row*.

| | | **Social test partners** | | **Non-social test partners** | |
|---|---|---|---|---|---|
| | | **Unfamiliar dog** | **Familiar dog II** | **Unfamiliar object** | **Familiar object** |
| **Social test partners** | **Familiar dog I** | p = 0.102 | p = 0.448 | **B ± SE = 0.403 ± 0.093 $t_{112}$=4.356 p<0.001** | **B ± SE = 0.368 ± 0.093 $t_{112}$=3.977 p=0.001** |
| | **Unfamiliar dog** | - | p = 0.561 | p = 0.286 | p = 0.448 |
| | **Familiar dog II** | - | - | **B ± SE = 0.265 ± 0.091 $t_{112}$=2.899 p=0.036** | p = 0.090 |
| **Non-social test partners** | **Unfamiliar object** | - | - | - | p = 0.701 |

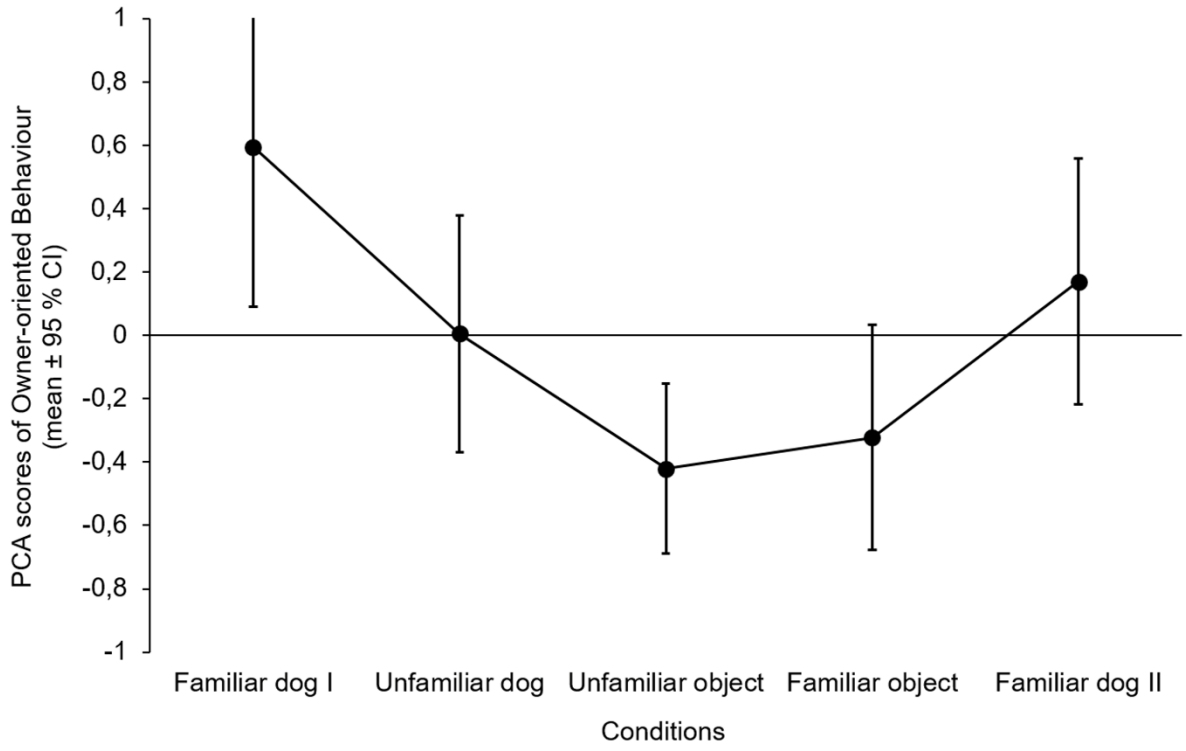


**Figure 3.2.** PCA scores of the *Owner-oriented Behaviour* principal component in different conditions. Figure shows the original PCA scores before Box-Cox transformation. The order of Unfamiliar dog, Unfamiliar and Familiar object conditions were counterbalanced between subjects.

There was a significant difference among conditions in *Test Partner-oriented Behaviour* ($F_{4,112}$=9.625, p<0.001). Subjects showed more *Test Partner-oriented Behaviour* in the Unfamiliar dog condition than in any other conditions; and also showed more behaviour in the Familiar dog II condition compared to the Familiar object condition (Table 3.4; Figure 3.3).

**Table 3.4.** Comparison of the emergence of *Test Partner-oriented Behaviour* between conditions (linear GLMM; significant differences are indicated with coloured background). For significant explanatory variables in the final models, we provide contrast estimates (B ± SE) and t values. Familiar dog I stands for the first, Familiar dog II stands for the last trial. Direction of difference is *Columns* vs *Row*, i.e. behaviour was more/less emphasized in *Column* compared to *Row*.

| | | **Social test partners** | | **Non-social test partners** | |
|---|---|---|---|---|---|
| | | **Unfamiliar dog** | **Familiar dog II** | **Unfamiliar object** | **Familiar object** |
| **Social test partners** | **Familiar dog I** | **B ± SE = -0.562 ± 0.128** **$t_{112}$ = -4.381** **p < 0.001** | p = 0.334 | p = 0.825 | p = 0.539 |
| | **Unfamiliar dog** | - | **B ± SE = 0.352 ± 0.127** **$t_{112}$ = -2.779** **p = 0.038** | **B ± SE = 0.590 ± 0.127** **$t_{112}$ = 4.652** **p < 0.001** | **B ± SE = 0.714 ± 0.127** **$t_{112}$ = 5.631** **p < 0.001** |
| | **Familiar dog II** | - | - | p = 0.256 | **B ± SE = 0.362 ± 0.124** **$t_{112}$ = 2.924** **p=0.029** |
| **Non-social test partners** | **Unfamiliar object** | - | - | - | p = 0.539 |

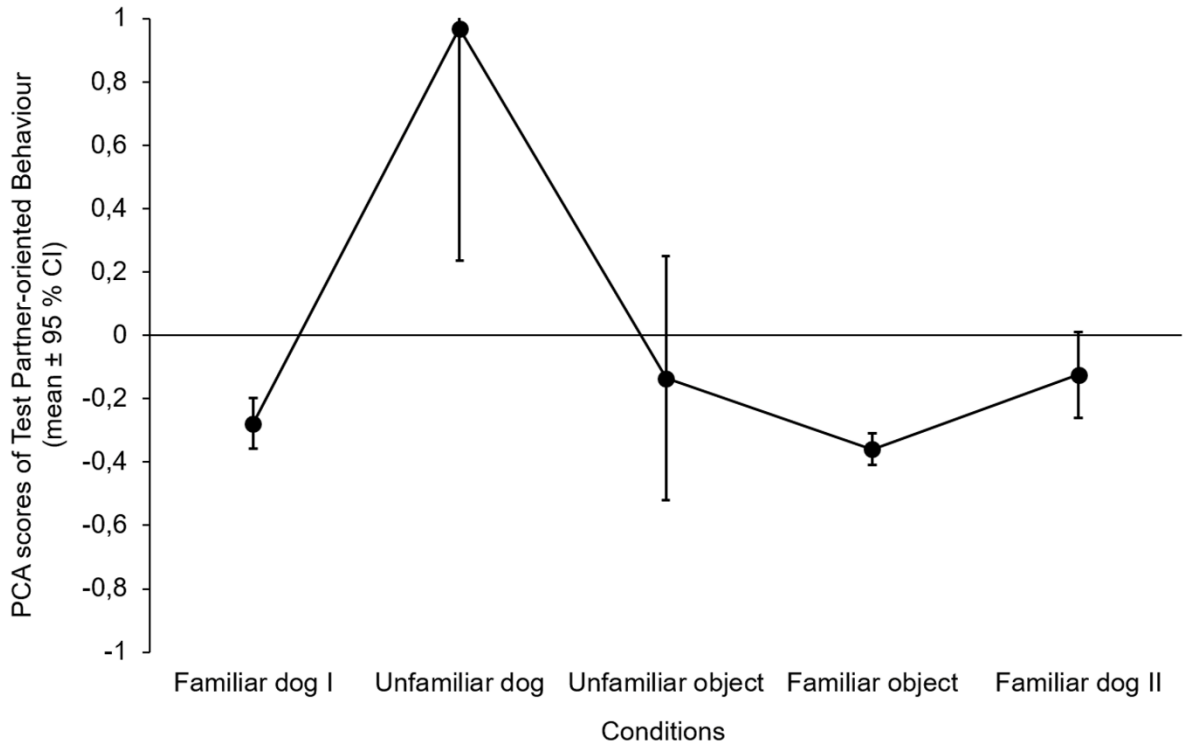


**Figure 3.3.** PCA scores of the *Test Partner-oriented Behaviour* principal component in different conditions. Figure shows the original PCA scores before the Box-Cox transformation. The order of Unfamiliar dog, Unfamiliar and Familiar object conditions were counterbalanced between subjects.

Results of the Friedman test show that dogs tried to interrupt the owner-test partner interaction more often in case of social, compared to non-social test partners (N=22, $\chi^2(4)=30.817$, $p<0.001$); however, there was no difference either within the social test partners or within the non-social test partners (Table 3.5, Figure 3.4).

**Table 3.5.** Comparison of attempts to interrupt the owner-test partner interaction between conditions (Friedman test; significant differences are indicated with coloured background). Familiar dog I stands for the first, Familiar dog II stands for the last trial. Direction of difference is *Columns* vs *Row*, i.e. behaviour was more/less emphasized in *Column* compared to *Row*.

| | | **Social test partners** | | **Non-social test partners** | |
|---|---|---|---|---|---|
| | | **Unfamiliar dog** | **Familiar dog II** | **Unfamiliar object** | **Familiar object** |
| **Social test partners** | **Familiar dog I** | Z = -0.500<br>p = 1.000 | Z = -0.295<br>p = 1,000 | **Z = -1.682**<br>**p = 0.004** | **Z = -1.841**<br>**p = 0.001** |
| | **Unfamiliar dog** | - | Z = -0.205<br>p = 1.000 | Z = -1.182<br>p = 0.132 | **Z = -1.341**<br>**p = 0.049** |
| | **Familiar dog II** | - | - | **Z = 1.386**<br>**p = 0.036** | **Z = 1.545**<br>**p = 0.012** |
| **Non-social test partners** | **Unfamiliar object** | - | - | - | Z = -0.159<br>p = 1.000 |

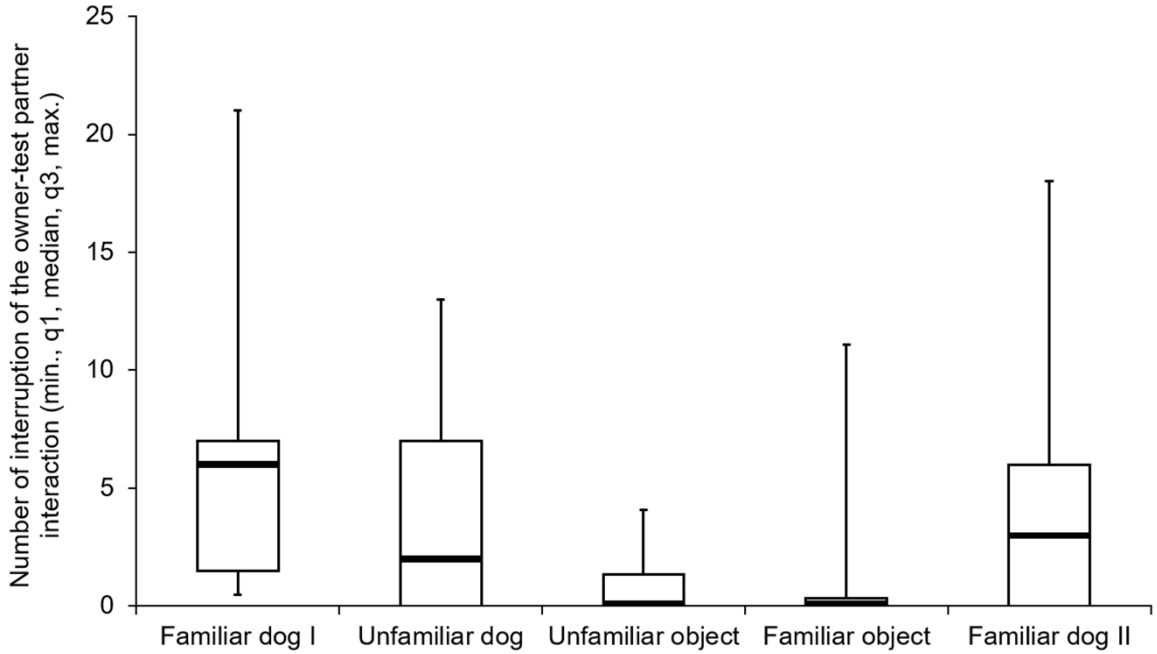


**Figure 3.4.** Number of attempts to interrupt the interaction between the owner and test partner in different conditions. The order of Unfamiliar dog, Unfamiliar and Familiar object conditions were counterbalanced between subjects.

Trials, order of conditions and dominance rank did not have an effect on *Interaction-*, *Test Partner-* and *Owner-oriented Behaviours* (*Interaction-oriented behaviour*, Trials: $F_{3,109}=1.069$, $p=0.365$, Condition order: $F_{5,104}=0.567$, $p=0.725$, Condition x Dominance rank: $F_{4,73}=1.214$, $p=0.312$, Dominance rank: $F_{1,77}=0.042$, $p=0.838$; *Test Partner-oriented behaviour*, Trials: $F_{3,109}=1.492$, $p=0.221$, Condition order: $F_{5,107}=1.262$, $p=0.286$, Condition x Dominance rank: $F_{4,73}=1.087$, $p=0.370$, Dominance rank: $F_{1,77}=0.151$, $p=0.699$; *Owner-oriented behaviour*, Trials: $F_{3,109}=2.110$, $p=0.103$, Condition order: $F_{5,104}=0.145$, $p=0.981$, Condition x Dominance rank: $F_{4,73}=0.334$, $p=0.854$, Dominance rank: $F_{1,77}=0.657$, $p=0.420$).

### 3.1.3. Discussion

Dogs showed more jealous behaviour in case of social compared to non-social test partners, discriminating between the two groups of potential rivals. Considering that dogs were interested in the owner-unfamiliar object interaction as well, but did not show jealous behaviour (based on our definition; see Section 3.1.), we suggest that the loss of owner's attention is not enough by itself to elicit the behaviour, but dogs take into account whether the social relationship is threatened by a social agent. Thus it seems that social test partners might be considered as potential rivals from the viewpoint of the relationship with the owner. Regarding that the number of trials and order of conditions did not have an effect on dogs' behaviour, and that subjects showed similar behaviour in both familiar dog trials, we can conclude that jealous behaviour is stable over time. Dogs showed functionally similar behaviour as observed in children under two years of age in similar situation that has been referred to as jealousy (Hart et al. 1998, 2004; Hart and Carrington 2002; Mize and Jones 2012; Mize et al. 2014; Hart 2016).

We suggest that test partner-oriented behaviour displayed toward the unfamiliar dog is (at least partially) independent from the jealousy-evoking situation, and dogs were interested in the unfamiliar dog in general. In case of jealousy we would expect agonistic behaviour (e.g. bite attempts, snapping, pushing away the test partner) as test partner-oriented behaviour, because the main function of aggression is to divide resources (Miklósi 2015); however, we did not find evidence for this in the present study (for similar observation see also Prato-Previde et al. 2018a, b). We suggest that the lack of agonistic behaviour is the result of many owners not allowing their dogs to be aggressive with other dogs. Aggressive behaviour found by Harris and Prouvost (2014) may also suggest that dogs did not accept the stuffed dog as a real one. However, we cannot exclude that the lack of agonistic behaviour was the result of the unfamiliar situation. The result indicates that the type of social test partner is crucial to study jealous behaviour in dogs (see below).

In the previous experiment conducted with dogs, Harris & Prouvost (2014) found longer look at the test partner only in the presence of the social test partner, but looking duration at the owner and number of attempts to interrupt the owner-test partner interaction did not differ between the social and unfamiliar non-social test partners. However, the latter two behaviours are part of the jealous behaviour, thus we would expect their emergence only in case of a social test partner, i.e. in the presence of a rival against which the subject can lose the relationship. Prato-Previde et al. (2018b) did not find difference in dogs' behaviour in the presence of the fake dog and unfamiliar non-social test partner either. In contrast, our data show that dogs discriminate between social and non-social test partners regarding their behaviour oriented

toward the owner, and trying to separate him/her from the test partner. Further, we only found enhanced behaviour oriented toward the test partner in case of the unfamiliar social test partner (see above our argument whether it is part of jealous behaviour). Thus it is possible that in the study of Harris & Prouvost (2014) subjects did not consider the stuffed dog as an animate or inanimate agent which is also strengthened by the investigation of Prato-Previde et al. (2018b). We propose that the procedure applied in the present study is a better approach to investigate the phenomenon, by using real dogs as social test partners (see also Prato-Previde et al. 2018b, a). Although the results of Prato-Previde et al. (2018a) (using real dog as social rival) could not confirm significant difference between jealousy-evoking vs control situations, it could be the artefact of method applied or individual differences might have prevented the manifestation of jealous behaviour. In their control group both dogs were present in the room, while the owner was reading. Although from the viewpoint of subjects it could be considered as merely the loss of attention of the owner (as argued by the authors), the presence of their potential rival dog could still poses a "threat". Based on all the above findings, we suggest that in future studies real dogs should be used as social test partners, but more investigation is needed whether the level of familiarity of the other dog (e.g. living together with the test partner, only meeting with it several times during the week, or knowing it only for a few hours before testing) has an effect on dogs' behaviour in such situation.

Territorial aggression and dominance rank within the household has been suggested to explain the behaviour displayed by dogs in such situations (see Morris et al. 2008). Considering that we tested dogs at an unfamiliar place, territorial aggression can be excluded as a causal factor. Similarly, the absence of any association with rank (indicated by the owner) makes it less likely that the displayed behaviour was elicited by dominance aggression. The experimental arrangement makes it unlikely that protectiveness, playfulness and boredom could be major factors. In case of protectiveness, we would not expect jealous behaviour when the test partner is the other dog from the household, and in case of playfulness and boredom we would have observed the behaviour in the presence of non-social test partners as well. However, it should be noted that we did not use a stranger person to control for the relationship with the owner despite it would be an important aspect. The results of Prato-Previde et al. (2018b) suggest that dogs behave similarly when a stranger and not the owner attends to the social test partner (i.e. the behaviour is not elicited due to the threat of the relationship), but this may be an artefact of the procedural design applied in that study (fake dog as test partner). Testing dogs' behaviour when not the owner but a stranger is focusing on the test partner would be important by using real dogs as social test partners, to be able to draw further conclusions.

Assessing jealous behaviour using Tinbergen's four questions is rather difficult at this point regarding the current (lack of) knowledge on its emergence and background. In the dissertation, we used a functional approach to study the behaviour due to its significance in fitness and survival (see Section 4 for more details regarding the function of the behaviour). Based on our results it seems that dogs show jealous behaviour just like humans; however, we do not know whether this behaviour can be traced back to their wolf ancestor or it is the result of domestication. Further, the lack of information about its emergence in other non-human species hinders to draw conclusions about its evolutionary origin. Researchers found that humans at six months of age already display jealous behaviour (Hart and Carrington 2002); however, no studies have been conducted to investigate its presence in younger infants. Unfortunately, we also have no information about the mechanisms underlying this phenomenon. However, here we would like to raise an important issue. In previous studies with dogs, authors have referred to jealousy in dogs and human children below two years of age, as a primordial form of jealousy, and that it occurs with different complexity across species (and, at least in humans, across age). Note however, that jealousy may not be an all-or-none phenomenon (see Prato-Previde et al. 2018b), and there are still several unanswered questions in humans as well: Is jealous behaviour emerging in humans and (potentially) non-human species driven by the same cognitive mechanism? Is jealousy triggered in different situations (e.g. parent-offspring or romantic relationship) driven by the same cognitive mechanism (see Harris and Darby 2003; Volling et al. 2013)? Is jealous behaviour in human children comparable to that in adult humans (see Harris and Darby 2003; Volling et al. 2013)? What drives individual differences in displaying jealous behaviour? These were just a few examples, but based on these uncertainties in our basic knowledge about jealousy, we suggest caution discussing its complexity and labelling it as *primordial form* without further information.

FMRI studies conducted in order to investigate jealousy would be important (Cook et al. 2018), however, the procedure should be planned more carefully including conducting previous, more detailed behaviour studies. Although it is important to note that fMRI studies only contribute to reveal the underlying neural activity, but they do not explain the mental state alone. Based on our results, we suggest that a real dog is required as potential rival to be able to trigger jealous behaviour, and the owner focusing attention to the other dog without giving it food would also be important. Analysis of activation in multiple brain areas would also be crucial due to the complexity of the behaviour (see also Takahashi et al. 2006; Harmon-Jones et al. 2009; Kelley et al. 2015; Harmon-Jones and Harmon-Jones 2018). Note that neural activity connected to jealousy in humans are all derived from research on romantic/sexual

relationships, and we do not know whether jealousy in such situation is comparable to jealousy emerging in other relationships. Thus comparative research should focus on the potentially different cognitive mechanisms underlying jealous behaviour displayed in these contexts.

Dogs' behaviour in the present study fulfil the functional description of jealousy; however, it can be argued whether the underlying emotional state shares similarities with the corresponding human emotion. Authors often focus on the emotional state underlying the behaviour, despite it being obscure in human children and adults in contrast to the observable behaviour. We suggest that a behaviour-centred approach may be more fruitful in the future, and this also facilitates comparative investigations.

# 4. PERCEPTUAL ANIMACY: LOW LEVEL RECOGNITION OF THIRD-PARTY INTERACTION

Social evaluation and jealousy both include complex behaviours thus it is difficult to determine which aspects of the observed behaviours are important for the third-party individual. Stimuli triggering animacy perception, on the other hand, can be described by simpler parameters (e.g. speed and direction of motion), and some motion patterns that has been described to elicit perceptual animacy can only be interpreted in third-party context (e.g. observation of chasing event).

Quick perception of animate entities is crucial both from the viewpoints of fitness and survival. The detection can be based on, for example, the look of the agents, but on their motion as well. In the present series of research, we have focused on the latter issue.

Based on the above, it is advantageous to spontaneously perceive moving entities as animate based on specific motion parameters, even without organism-shaped body or motion pattern having higher complexity (see biological motion; Johansson 1973) (e.g. Heider and Simmel 1944; Tremoulet and Feldman 2000; Blake and Shiffrar 2007). Observers' tendency to spontaneously recognize inanimate objects as animate based on simple motion cues has been referred to as *perceptual animacy* (e.g. Scholl and Tremoulet 2000; Tremoulet and Feldman 2000; Gao et al. 2009; Meyerhoff et al. 2013). Adult humans, for example, tend to describe even a single moving geometric figure as animate based on simple motion cues, such as simultaneous change in speed and direction without visible external cause (Tremoulet and Feldman 2000). However, it seems that based on temporal contiguity and spatial proximity, not only animacy, but personality traits, emotions and intentions are also attributed by adult humans to moving geometric figures (Heider and Simmel 1944; Bassili 1976). The study of Barrett et al. (2005) further suggest that the recognition of specific motion patterns performed by inanimate objects is irrespective of culture (German vs Shuar participants).

Gao et al. (2009) suggested that there are different types of perceived animacy based on the motion pattern itself (e.g. chasing or fighting) that are driven by different types of cues. In case of some of these patterns (e.g. chasing) animacy can be perceived (or at least perception is enhanced) based on the interaction between objects. This can be a form of interpreting third-party interaction and it provides information not only on their states (animate or inanimate), but in case of recognition of the pattern itself, about their possible future behaviour

as well. For example, animacy perception can help prey to become more vigilant to animate agents in the environment.

Although objects that display self-propelled motion are described as *only* animate, the attribution of goal-directed motion is related to agency (Blakemore et al. 2003; Luo et al. 2009; Rosa-Salva et al. 2016). It is important to note however, that these two concepts cannot be fully separated as animacy can be perceived without goal-directed behaviour, but attributing agency always involves the attribution of animacy (Gao and Scholl 2011, but see Gobbini et al. 2011 who included inanimate automatons in the domain of agents). Currently there are two main hypotheses regarding animacy perception (see Tremoulet and Feldman 2006): (1) intentionality hypothesis claims that animacy can only be perceived when intentionality is present as well (Bassili 1976; Dittrich and Lea 1994; Gelman et al. 1995); and (2) Newtonian violation hypothesis suggests that the perception of an internal energy source is the key for animacy perception (Bingham et al. 1995; Tremoulet and Feldman 2000; Kaduk et al. 2013). Thus while in the former case context can modify the perception of animacy, in the latter case it depends solely on the motion of the objects (see Tremoulet and Feldman 2006). There is no agreement on this debate to date.

There is some disagreement whether animacy perception relies indeed on visual perception or it involves complex mental processes (see also the debate on whether cognition can have an effect on perception in general, in Firestone and Scholl 2016). Scholl and Gao (2013) reviewed several studies with different research methods to address this question. These included experiments conducted with adult humans in which participants either had to describe the observed motion (e.g. Tremoulet and Feldman 2000; Gao et al. 2009; Meyerhoff et al. 2013), researchers tested their behavioural response (e.g. Gao et al. 2009, 2010; Gao and Scholl 2011), or they measured activation of specific brain areas (e.g. Castelli et al. 2000; Blakemore et al. 2003; Schultz et al. 2005; Tavares et al. 2008; Gao et al. 2012; for a review see e.g. Heberlein 2008). Such results imply that animacy perception most probably reflects specialized processing in the visual system, and it is not related to complex cognitive attributions (see also Rutherford 2013). This is also supported by the findings of Di Giorgio et al. (2017) and Mascalzoni et al. (2010) who found evidence on animacy perception in new-born babies and newly hatched chicks (*Gallus gallus domesticus*) (respectively) (see below).

*Chasing* is one of the most often used motion pattern to study the phenomenon, because it contains information that can elicit the perception of animacy (and agency). It involves self-propelled motion and violation of Newtonian mechanics, but goal-directed motion and non-mechanical contingency are also general characteristics of it (e.g. Rochat et al. 1997, 2004;

Gao and Scholl 2011; Scholl and Gao 2013). Another important aspect is that the chasing pattern (parameters of the motion) is relatively easy to manipulate systematically (Nahin 2007; Scholl and Gao 2013). According to Scholl and Gao (2013), animacy may be detected via several independent cues (similarly to depth perception) the effect of which should be tested separately; however, they further suggested that interaction among the objects is an important aspect. Considering that we do not know clearly which characteristic of the motion elicit the perception (whether cues to animacy are enough or features specific to agency are required as well; see Tremoulet and Feldman 2006), and that goal-directedness can be considered as the subset of animacy (see Gao and Scholl 2011), here we refer to the perception of *animacy*, not *agency*.

Chasing can be important in between and within species interactions as well, including different contexts like play or predation (Barrett et al. 2005), thus the utilization of this motion pattern is suitable to study animacy perception in non-human species and to conduct comparative research.

In studies conducted with human infants and adults, researchers used two-dimensional video and interactive displays that relied on the visual perception of participants. They used chasing-like motion as specific (dependent) movement pattern performed by inanimate agents (geometric figures) that could give rise to the spontaneous perception of a social event based simply on motion information (e.g. (Rochat et al. 1997, 2004; Szego and Rutherford 2007; Gao et al. 2009; Gao and Scholl 2011; Meyerhoff et al. 2014a; Galazka et al. 2016; Parovel et al. 2018). Rochat and colleagues (1997) presented the side-by-side video display of chasing and independent motions to human infants and adults, and measured looking duration toward the stimuli. They found that three-month-old infants already discriminate between the patterns. However, while at this age they look longer at the chasing motion, infants of five months of age and adults look longer at the independent pattern. One may raise the question why preference in looking at the independent pattern indicates the perception of the chasing motion as animate motion. Authors suggested that looking times at the patterns were influenced by the quick perception of the chasing pattern which led to rapid habituation resulting in a shift in look toward the more unfamiliar, "puzzling" pattern (Rochat et al. 1997; see also our argument in case of our own studies). Results also revealed that 5-month-olds showed more frequent gaze alternation between patterns than 3-month-olds, which authors explained by 5-month-olds being more engaged in comparing the patterns. However, other explanations should not be excluded, for example, different visual attention or processing of visual information. Helo et al. (2016) found that duration of fixation on visual scenes decreases with age in human infants, but

there was no significant difference between infants of three to nine months of age in their scenario. It should also be noted that Galazka and Nyström (2016) found that 12-month-old infants, but not 5-month-olds show looking preference toward spatially proximate objects, similarly as adult humans.

The measure of looking duration at stimuli is a widely used procedure, but it only provides indirect access to the underlying mental processes and how it reflects behaviour function in real situations. Other widely used methods to investigate whether participants detect a chasing-like pattern in such displays is by asking them to rate the stimuli, or directly about their thoughts on the stimulus (e.g. Heider and Simmel 1944; Rochat et al. 1997; Tremoulet and Feldman 2000; Meyerhoff et al. 2013, 2014b). For example, in the so called *Find-the-Chase* task adults watched video displays of moving geometric shapes and they had to report whether they perceived chasing in the displays (Gao et al. 2009; Meyerhoff et al. 2013, 2014b). In other studies, participants had to describe in details what they watched and their response was evaluated based on the wording they used (e.g. words invoke the notions of animacy or using neutral words) (e.g. Heider and Simmel 1944; Gao et al. 2010). In some cases, these methods are combined with the measurement of subjects' looking pattern toward the stimuli (e.g. Rochat et al. 1997).

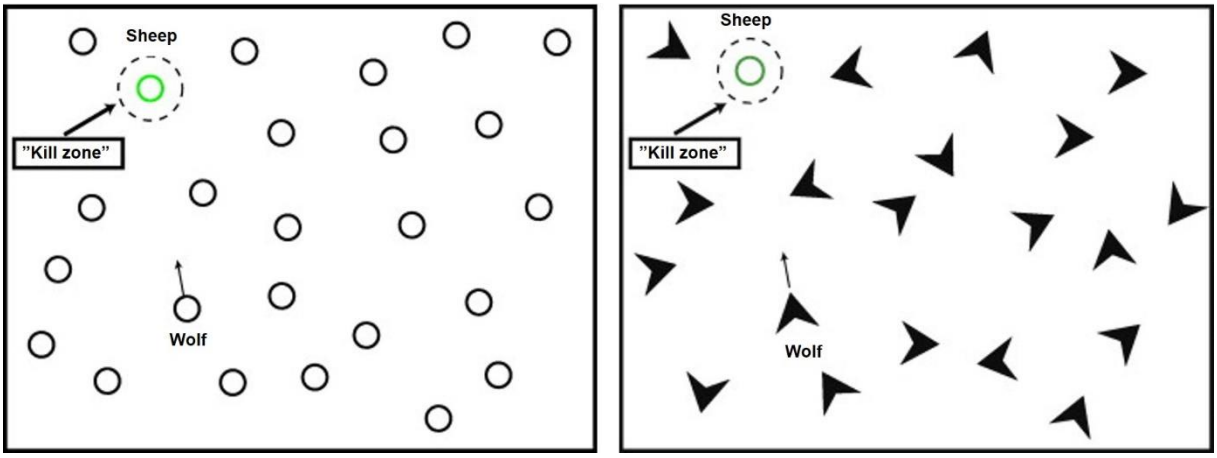


**Figure 4.1.** Illustration of the *Don't-Get-Caught!* task from Gao et al. (2009). *Sheep* refers to the chasee, and *wolf* to the chaser. *"Kill zone"* indicates the area within which the chaser catches the chasee.

Although the above methods are widely accepted and provide important information on the phenomenon, they do not allow a clear separation of perception and cognition as the underlying process which is a main interest in this research area (Scholl and Gao 2013). In a series of studies Gao and colleagues (Gao et al. 2009, 2010; Gao and Scholl 2011) used the *Don't-Get-Caught!* task to test whether participants can pinpoint the chaser among many moving agents with the same physical properties. In this task, participants had to avoid the chaser by controlling one of the figures on the screen and they could only rely on the motion characteristics of the chaser to succeed (see Figure 4.1; Gao et al. 2009; Gao and Scholl 2011). Authors proposed that the *Don't-Get-Caught!* task serves as a better approach to study visual perception in relation to animacy detection, because it measures participants' perception more objectively and we can also obtain information about the effect of the percept on subjects' behaviour (Gao and Scholl 2011). They modified different parameters of the motion (e.g. speed, proximity and deviation from heat-seeking chasing), and the shape of the geometric figures (from dot to arrow-like figure that has perceived orientation) to test how these features influence perception of the chasing pattern. Results revealed that heat-seeking pursuit (0°-30° deviation from perfect heat-seeking; Figure 4.2) and directionality in the movement of the figure (chaser is oriented along the direction that it moves) facilitated the spontaneous identification of the chaser. They further found that temporal deviation (interruption) from the perfect chasing also decreases or prevents the possibility to perceive the chaser (Gao and Scholl 2011). These studies suggested that speed, frequency of change in direction and deviation from perfect heat-seeking are important features for human observers to perceive animacy. By using different method, Szego and Rutherford (2007, 2008; see also Rutherford 2013) also found association between the perception of speed and animacy (higher speed facilitates animacy perception). Frankenhuis et al. (2013; similar method as Rochat et al. 1997) reported that human infants are sensitive to attraction and frequent turns, but results are not that clear in case of acceleration; however, it is important to note that their results may be affected by the attentiveness of subjects (see also Rochat et al. 1997 who found differences within age groups based on infants' overall looking duration toward the display).

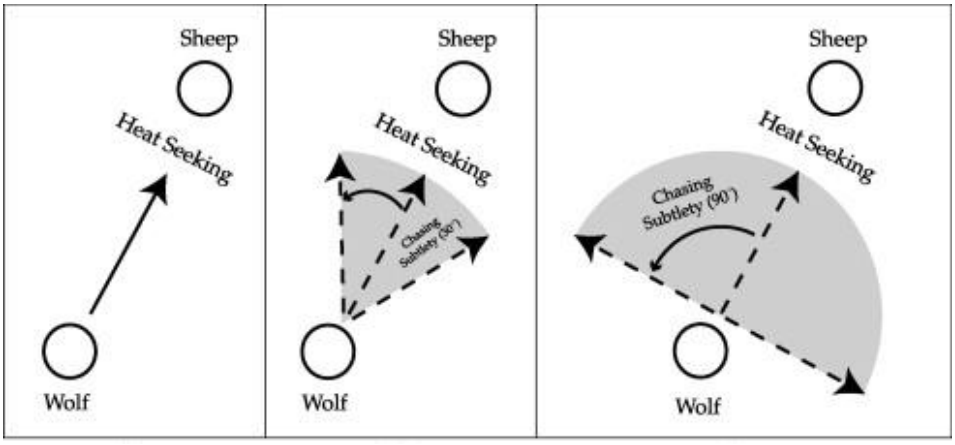


**Figure 4.2.** Illustration of angle of pursuit from Gao et al. (2009). *Sheep* refers to the chasee, and *wolf* to the chaser.

Thus overall it seems that spatiotemporal contingencies trigger the impression of specific motion pattern, such as chasing, in humans. Recent research also found that newborn human infants are already sensitive to self-propelledness, which suggest an inborn predisposition to these cues (Di Giorgio et al. 2017). However, based on its biological significance, perceptual animacy could be a common phenomenon in a wide range of non-human animals. Unfortunately, only a few studies have investigated animacy perception in species other than humans, to date (Goto et al. 2002; Mascalzoni et al. 2010; Atsumi and Nagasaka 2015; Rosa-Salva et al. 2016).

So far two studies have used chasing motion pattern to study the phenomenon in non-human species, both of which used two-dimensional displays applying the go/no-go discrimination task (which requires initial training). Neither in pigeons (*Columba livia*) (Goto et al. 2002), nor in squirrel monkeys (*Saimiri sciureus*) (Atsumi and Nagasaka 2015) authors could provide convincing evidence on whether subjects perceived the specific interaction among the agents, a dependent motion pattern. Further, we suggest that the use of training when investigating perception makes it difficult to separate whether the observed behaviour of subjects is due to the perception of the specific features of the motion or they used another strategy related to their initial training (e.g. memorizing the pattern itself). A better approach has been applied with newly hatched chicks (Mascalzoni et al. 2010; Rosa-Salva et al. 2016), in which subjects' preferential approach to one of two stimuli was tested (note that they only used self-propelled motion and speed changes, not chasing pattern). Results confirmed that similarly to newborn human infants (Di Giorgio et al. 2017), naïve chicks also prefer self-propelled geometric figures to those moving with constant speed or their motion is the result of physical contact.

As mentioned above, we propose that animacy perception should be a common phenomenon in animals; however, evidence is rare. Considering the general mammalian homology, and that in canids chasing plays a key role in acquiring food, we hypothesised that dogs are able to spontaneously perceive animacy similarly to humans. In all experiments we used dependent and independent motion patterns performed by inanimate objects. The dependent motion pattern was designed following the characteristics of motion patterns described as chasing in previous studies (e.g. Gao et al. 2009; Gao and Scholl 2011). Thus in the following we will refer to the dependent motion as *chasing*; although we would like to emphasise that we do not claim that subjects recognized the chasing pattern *per se*. In case of the independent patterns we designed the motion of the objects to have similar dynamics as the ones involved in the chasing interaction to avoid that other visual factors (e.g. salience of speed change) can be accounted for differential behaviour showed toward the patterns.

## 4.1. Comparative approach to the perception of animacy

We tested whether dogs are able to discriminate between dependent (chasing) and independent movement patterns; for cross-species comparison, we also tested adult humans in the same set-up using the same stimuli. We applied similar method as used by Rochat et al. (1997), and displayed side-by-side chasing and independent motion patterns performed by moving geometric figures (dots). We hypothesised rapid habituation to the chasing pattern over time both in humans and dogs that would result in decreased looking duration toward the chasing, and increased look at the independent ("puzzling") pattern.

### 4.1.1. Method

#### Constructing stimuli

We used the side-by-side displays of chasing and independent movement patterns by two white dots over a plain black background. The movement patterns were separated by a white vertical line in the middle of the screen (Figure 4.3). Stimuli were created by the ChasingDots program developed by Bence Ferdinandy. The program generated four different types of videos at the same time: chasing pattern alone, independent motion alone, chasing-independent pair and independent-chasing pair. Hereafter, we will refer to the first two as *patterns*, the latter two

as *stimuli*, and the video displayed to subjects (including the attention grabbers and two stimuli; see below) as *video*.

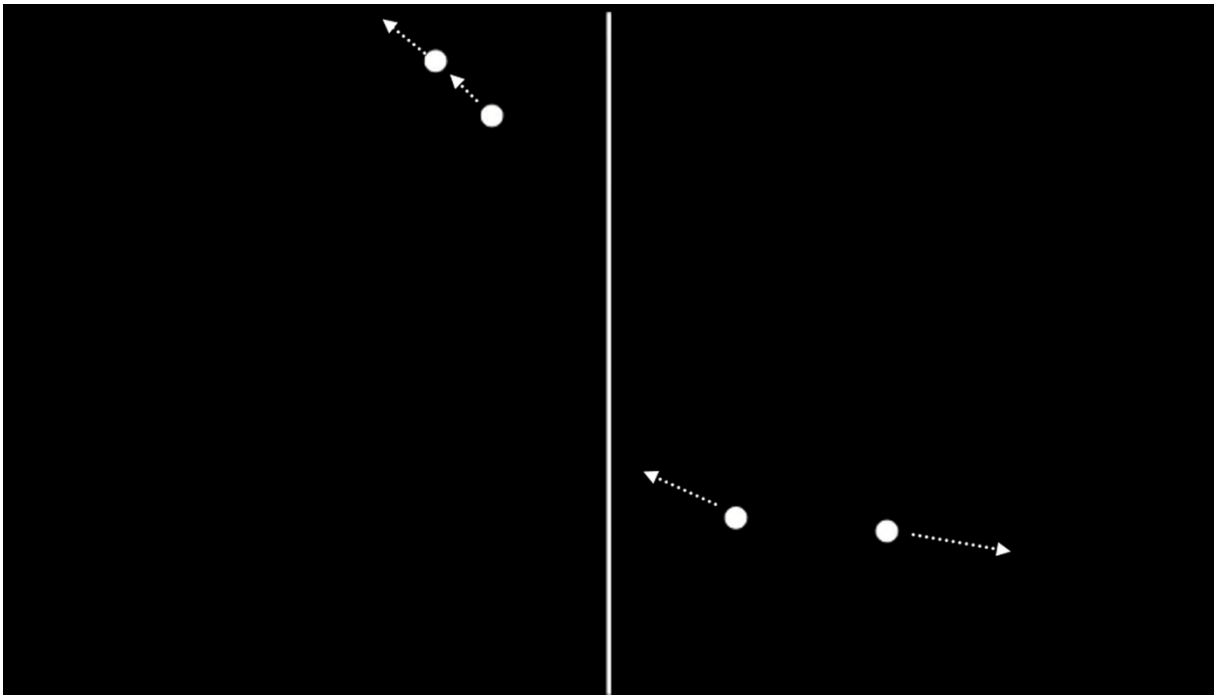

Figure 4.3. Snapshot from the displayed video. On the left side of the picture the dots are chasing each other, while on the right side two dots are moving independently from each other. Sides of the chasing and independent patterns are separated by a white vertical line. Dotted arrows show the direction of movement.

Chasing motion patterns were generated based on previous findings (e.g. Tremoulet and Feldman 2000; Gao et al. 2009; Gao and Scholl 2011). The chaser moved directly toward the chasee (heat-seeking pursue) and accelerated by a given probability in every second. Whenever the chaser got closer to the chasee than a specified distance, the chasee accelerated until it reached a given distance from the chaser. For the parameters applied to generate the chasing pattern, see Table 4.1. Independent movements were compiled from two other chasing movements with the same parameters: from one of them the program used the chaser, and from the other one the chasee. This way we ensured that in any given stimuli the independent and chasing patterns are similar in all parameters (i.e. in their dynamics), except for the movements of the two dots in relation to each other.

**Table 4.1.** Description and values of the parameters used to create the stimuli in the ChasingDots program

| Parameter | Value | Description |
|---|---|---|
| **Basic parameters** | | |
| **Boundary** | 13 px (pixel) | The width of the invisible border region along the edges of the screen that both the chaser and chasee avoid |
| **Corner radius** | 180 px | The radius of the circle that gives the curvature of the corners of the invisible border |
| **Framerate** | 100 fps (frame per second) | The framerate of the output videos and the refresh rate of the interactive window |
| **Dot size** | 12 px | Radius of the dots (chaser and chasee) |
| **Separation size** | 4 px | The width of the white vertical line between the two movement patterns |
| **Parameters of the chasing stimuli** | | |
| **Starting distance** | 400 px | Initial distance between the chaser and the chasee |
| ***V* chasee** | 220 px/s | Basic speed of the chasee |
| ***V* chasee acceleration** | 340 px/s | Speed of the chasee when it accelerates |
| **Acceleration distance** | 50 px | The chasee accelerates when the chaser is closer than the given value |
| **Calm distance** | 110 px | The chasee goes back to its basic speed after acceleration when it reaches the given distance from the chaser. |
| **Turn probability** | 0.7 | The probability that the chasee will take a turn in a given second |
| **Min turn angle** | 45º | The minimum angle of the turn of the chasee |
| **Avoid angle** | 180º | The angle of the triangle centred on the chaser-chasee line. The chasee avoids this triangle as a direction |
| ***V* chaser** | 230 px/s | Basic speed of the chaser |
| ***V* chaser acceleration** | 310 px/s | Speed of the chaser when it accelerates |

| | | |
|---|---|---|
| **Acceleration probability** | 0.95 | The probability that the chaser accelerates in a given second |
| **Acceleration time** | 1.8 s | The duration of the chaser's acceleration |
| **Proximity boundary** | 35 px | The chaser cannot go closer to the chasee than the given value |

In order to avoid the direct contact among dots, the program generated an invisible circle around the chaser with a specified radius that the chasee could not cross (proximity boundary; see Table 4.1). If the chasee reached this circle it continued its route in the same direction by leaving out the inner part of the circle (see Figure 4.4). In some cases, it appeared visually as a jump by the chasee. Considering that it could be a salient cue to call subjects' attention to one side of the screen, we excluded all videos in which this error has been detected (see below).

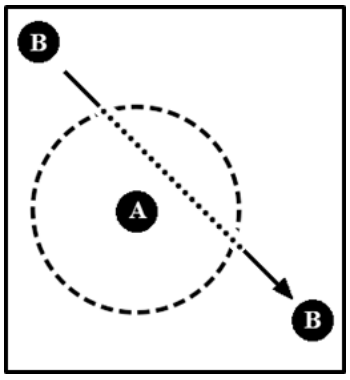


**Figure 4.4.** Proximity boundary. A - chaser; B - chasee. The dashed line indicates the radius boundary around the chaser; the dotted line indicates the part of the route that the chasee omits

In order to keep the chasing model simple, we chose a mathematical approach that involved relatively few variables to make it easier to comprehend. Our model was stochastic, resulting in some unintended salient cues appearing in both patterns. Instead of designing a more complex model we decided to exclude stimuli in which any of these issues appeared. We defined three unintended cues: (1) the above mentioned visual jump by the chasee that can appear in the chasing and independent patterns as well; (2) the randomly assigned chaser and chasee has direct contact in the independent motion; and (3) in a few cases the chasee (in both patterns) can get stuck in a corner for a short time, bouncing back and forth. We continued to generate stimuli (a total of 200) until we reached a final number of 36 stimuli that did not contain any of the above issues (20 % more stimuli as we needed overall for the test).

We used a specific questionnaire to pre-test the patterns on university students. Each chasing and independent patterns was evaluated by two different students from two points of view; one of them had to report whether there was an interaction among the dots in the displayed pattern or not, while the other student had to choose one out of six possible interactions (following, chasing, dancing, racing, fighting and copying) to describe the pattern. We excluded the chasing pattern if it was not described as chasing or following, or students indicated the lack of interaction among the dots. We excluded the independent pattern if students reported that there was an interaction among the dots. Patterns were tested alone without their pairs in the stimuli, however, excluding one pattern meant the exclusion of the stimuli containing this pattern (even if no reason for exclusion had been reported about the other pattern, as the program generated them in pairs).

We tested the first 26 chasing and independent patterns to reach the final number of 15 different stimuli that later had been used in the study (overall 30 videos because we counterbalanced between subjects the side on which the chasing pattern was first displayed). We presented the same set of stimuli (30 videos) to dogs and humans, and each stimulus was presented to one dog and one human participant.

All stimuli started with an audiovisual attention grabber to direct subjects' attention to the centre of the screen (duration: 2.32 s). The attention grabber was a baby rattle that swung side-to-side accompanied by a bell-like sound. We repeated the stimuli twice (Trial 1 and 2), between trials the screen remained black for 3 s.

## Formal description of the stimuli generating simulation

In each simulation we have a chasee and a chaser following some simple rules. Let us denote the coordinates of the chaser and the chasee by $\mathbf{r}_w$ and $\mathbf{r}_s$ respectively, the direction of their velocities with $\mathbf{n}_w$ and $\mathbf{n}_s$, the corresponding angles of these direction vectors with $\varphi_w$ and $\varphi_s$. In each step of the simulation the coordinates of the chaser and the chasee are updated as

$$\mathbf{r}_w\,(t + \Delta t) = \mathbf{r}_w\,(t) + \mathbf{n}_w\,(t) v_w \Delta t, \quad (1)$$

and

$$\mathbf{r}_s\,(t + \Delta t) = \mathbf{r}_s\,(t) + \mathbf{n}_s\,(t) v_s \Delta t, \quad (2)$$

where $\Delta t = 1/(n_s n_f)$, with $n_f$ denoting the framerate, and $n_s$ the number of steps in a frame.

The chaser and the chasee are bounded by a rectangle with the two sides being $L_x$ and $L_y$ long, but in general, they are not able to touch the wall, because there's an inner reflective boundary. This runs parallel with the walls at $d$ distance from them, making a smaller rectangle, but whose corners are rounded with circles of radii $R_d$. When either the chasee or the chaser

reaches this inner boundary it is reflected off the local tangent of the boundary. The outbound angle - with respect to the tangent - will be chosen from a uniform distribution between a simple reflection (same outbound as incident angle compared to the wall) and reflection perpendicular to the wall, thus having "sharper" turns than simple reflection.

These two rules form the basis of the dynamics of both the chasee and the chaser.

*Dynamics specific to the chaser*

The velocity of the chaser always points toward the chasee (except when overridden by getting too close to a wall).

The chaser can be in two states, either normal or sprinting. The chaser starts as being in its normal state. At each step the chaser may start a sprint with a probability of $p_s\Delta t$. When the chaser is in sprinting, the speed $v_w$ in Eq. 1 is changed to $v_{ws}$ for $t_s$ time.

*Dynamics specific to the chasee*

In each time step, the chasee may change the $\varphi_s$ with an angle uniformly chosen from $[-90°,-\Delta\varphi_m]\cup[\Delta\varphi_m, 90°]$ with a probability of $p_t\Delta t$. If at any time the angle obtained from this, or the angle obtained from getting too close to a wall would make $\mathbf{n}_s$ fall into an $\alpha$ wide angle originating from the chasee and centered on the line between the chasee and the chaser, $\varphi_s$ will be turned to the closest side of this angle, in order to avoid running deliberately into the chaser. Even then it might happen that the chaser catches up. To certainly avoid this, if the chasee is closer than $R_t$ to the chaser, it will "teleport" along the direction of its current velocity, until it is farther than $R_t$.

The chasee also has two states: normal and panic. The chasee will switch to the panic state when the chaser gets closer than $R_p$ and will leave this panic state once it manages to get further than $R_c$ from the chaser. While in the state of panic, the speed $v_s$ in Eq. 2 will be switched to the faster $v_{sp}$.

## Subjects

*Dogs*

Ethical approval was obtained from the National Animal Experimentation Ethics Committee (PEI/001/1492-4/2015). Owners provided a written consent form to voluntarily permit their dogs to participate in the study.

Overall we tested 40 dogs, of them 30 dogs remained in the final analysis (different breeds; 16 females; mean age ± SD 6.1 ± 3.4 years; see Table A2 in Appendix). We excluded three dogs due to procedural problems (problem with the displayed video or with the sound system, or the camera could not capture the dog's eyes), and seven dogs because they looked at the stimuli for less than 1 s in either of the trials.

Age did not have an effect on dogs' looking times (tested for the overall looking time at the screen, LMM: Age x Trial, $F_{1,28} = 1.498$, $p = 0.231$; Age, $F_{1,28} = 0.141$, $p = 0.710$). We only tested dogs whose owner did not report any problem regarding the dog's eyesight.

*Humans*

Ethical approval was obtained from the Institutional Psychological Ethics in Research Committee (EPKEB-2016/026). Participants (all of legal age) provided a written consent form that they participate in the study voluntarily.

We tested 31 university students; we had to exclude one participant due to the quality of the recording. Thus in the final analysis we had 30 human participants (19 females; mean age ± SD 21.9 ± 2.2 years; see Table A3 in Appendix). All participants had normal or corrected to normal vision.

## Apparatus

Participants were tested in a 5.2 m x 3 m test room at the Department of Ethology, Eötvös Loránd University. The video was projected on a screen (2 m x 2.1 m). The audio was displayed by two speakers centred behind the screen to avoid possible asymmetric cues. The projector was mounted on the ceiling behind the subject. Each trial was recorded by two cameras. One of them was a 25 frame per second (fps) zero lux camera (Panasonic NV-DS28) that can record in low light density. It was mounted on a compact tripod and placed before the screen, equal distances from its two sides. The topmost point of the camera was below the lowest point of the displayed stimuli. We used infrared LEDs directed toward the subjects to improve the visibility of their eyes for the zero lux camera. The infrared LEDs were placed right next to the zero lux

camera. The other camera was a synchronized camera on the ceiling behind the subject (above the projector). For the arrangement of the room see Figure 4.5.

### Procedure

After the owner and the dog entered the room, the owner sat on a chair placed in the room and hold the dog in front of him/her. Human participants sat on a pillow placed in the room before they entered so that their eyes got close to the height of the dogs' eyes. Subjects sat 2.8 m away from the screen (Figure 4.5). Experimenter (E) 1 adjusted the focus of the zero lux camera to capture the subjects' face and turned off the lights in the room. In case of dogs E1 stood behind the owner, whereas in case of humans she left the room. E2 started the video from outside. After the video ended E1 turned on the lights and the test ended. We asked the owner to look down during the test to rule out unintended human influence ('Clever Hans effect'; Pfungst 1911).

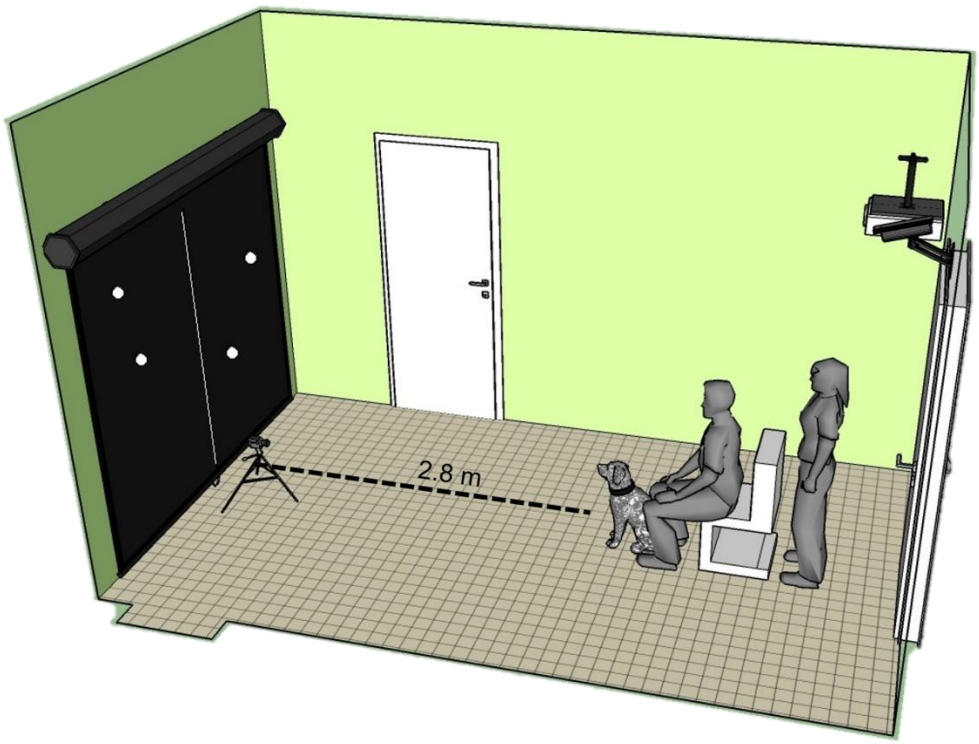


**Figure 4.5.** Experimental set up.

We showed subjects the simultaneous side-by-side display of chasing and independent motion patterns (see details above). We repeated the 10 s long stimuli twice (Trial 1 and 2). The sides of the chasing and independent patterns were counterbalanced between trials and subjects.

Stimuli in both Trial 1 and 2 started with an attention grabber to direct subjects' attention toward the centre of the screen. Between trials the screen remained black for 3 s.

### Data analysis

All tests were recorded and subjects' behaviour was analysed with Solomon Coder 15.11.19; videos were coded frame-by-frame (25 fps). We coded the looking direction of subject (chasing, independent or away) for each frame based on their eye movements.

From looking duration (length of looking at each patterns) we calculated looking time as proportion of trial time spent looking at each pattern, and used these (arcsine transformed) proportions as explained variables in statistical analysis. In dogs, the looking duration toward the stimuli in both trials was normally distributed after the arcsine transformation according to the visual inspection of the Q-Q plots and based on the Kolmogorov-Smirnov tests (Trial 1: Chasing $D_{30} = 0.135$, $p = 0.173$; Independent $D_{30} = 0.078$, $p > 0.200$; Trial 2: Chasing $D_{30} = 0.109$, $p > 0.200$; Independent $D_{30} = 0.070$, $p > 0.200$). Looking duration of humans was also normally distributed after the arcsine transformation of the data according the visual inspection of the Q-Q plots and also based on the Kolmogorov-Smirnov tests (Trial 1: Chasing $D_{30} = 0.116$, $p > 0.200$; Independent $D_{30} = 0.106$, $p > 0.200$; Trial 2: Chasing $D_{30} = 0.122$, $p > 0.200$; Independent $D_{30} = 0.096$, $p > 0.200$).

Statistical analysis was conducted using IBM SPSS Statistics 22. We used Linear Mixed Models (LMMs) to analyse the effects of motion pattern (*chasing* and *independent*), trial (*Trial 1* and *2*) and species (*dog* and *human*) on looking time. Initial models included all two- and three-way interactions between explanatory variables. We also used LMMs to analyse within-trial looking times of dogs and humans, separately for Trial 1 and 2. Backwards model selection was based on AIC values, so that the model with the lowest AIC value was kept and we considered a model better whenever delta AIC was $\geq 2$. For significant explanatory variables in the final models, we provide parameter estimates ($B \pm SE$), whereas for non-significant variables we provide test statistics before exclusion from the model.

To investigate within-trial dynamics of looking at stimuli, we constructed looking-time curves for both dogs and humans separately for both trials. We calculated the proportions of looking at the chasing and looking at the independent patterns for every consecutive three frames to create a single point of a curve. We present the proportions of looking at the screen for both dogs and humans (Figure 4.7 and 4.8). From this analysis it is apparent that there is an initial time when neither dogs nor humans look at the stimuli, thus for subsequent analysis, we disregarded data points before their looking at the stimulus proportion reached 80 % of their

respective averages (marked red on Figure 4.7 and 4.8). To capture overall trends we applied linear regression to the data (i.e. for the points after reaching the 80 % threshold), and provide the slope of the regression line (B ± SE).

We further analysed the frequency of changing the look between the two motion patterns by counting the number of change *from chasing to independent* and *from independent to chasing* (irrespectively of whether there was a delay in between). Based on the AIC values, we used loglinear GLMM for the analysis, because data fit best the Poisson distribution (model with the lowest AIC value was kept, we considered a model better whenever delta AIC was ≥ 2; AIC = 195.426). For significant explanatory variables, we provide parameter estimates (B ± SE).

Inter-coder reliabilities were investigated on random subsamples of the recordings by an independent coder (Tamás Faragó) who repeatedly coded 20 % of dog and 20 % of human subjects. We exported the full coding sheets of both coders from the Solomon Coder and checked the correspondence between the coders for all data points (i.e. about 500 data point pairs regarding the frame-by-frame coding of the videos recorded in 25 fps). We analysed the consensus between coders calculating Cohen's kappas (mean ± SD Cohen kappas, dogs: 0.734 ± 0.179; humans 0.787 ± 0.139).

### 4.1.2. Results

The difference between looking times at the two patterns changed with trials, as reflected by a *Trial x Pattern* interaction in our analyses (LMM of looking time, *Trial x Pattern*: $F_{1,235} = 13.590$, $p < 0.001$). This interaction was driven by subjects looking longer at the independent than at the chasing pattern in Trial 2 (Trial 2 vs Trial 1: Chasing → Independent: B ± SE = 0.199 ± 0.54, $p < 0.001$; see Figure 4.6); the results further suggest that this change in behaviour was the same in dogs and humans (i.e. no three-way interaction: *Trial x Species x Pattern*: $F_{1,232} = 0.050$, $p = 0.823$). *Species x Pattern* ($F_{1,233} = 0.336$, $p = 0.563$) and *Species x Trial* ($F_{1,234} = 0.712$, $p = 0.400$) interactions were non-significant, and therefore excluded from the final model. Total looking times toward the screen were different between dogs and humans (*Species*: $F_{1,235} = 13.590$, $p < 0.001$), because dogs looked shorter to the screen than humans (Dogs vs Humans, B±SE = 0.191±0.027, $p < 0.001$; for more details see below and Figure 4.7 and 4.8).

Within-trial looking times were different between the two species (LMM, Trial 1: $F_{1,117} = 28.981$, $p < 0.001$, Dogs vs Humans, B ± SE = 0.168 ± 0.031, $p < 0.001$; Trial 2:

$F_{1,117} = 23.337$, $p < 0.001$; Dogs vs Humans, $B \pm SE = 0.204 \pm 0.062$, $p = 0.001$), however, both dogs and humans reacted similarly to the patterns (LMM, Trial 1, *Species x Pattern*: $F_{1,116} = 0.482$, $p = 0.489$; Trial 2, *Species x Pattern*: $F_{1,116} = 0.047$, $p = 0.829$). Although in Trial 1 both species looked equally long relatively at the two patterns (*Pattern*: $F_{1,117} = 0.216$, $p = 0.643$), this changed for Trial 2 (*Pattern*: $F_{1,117} = 17.530$, $p < 0.001$) so that dogs and humans looked longer at the independent than at the chasing pattern (Trial 2, Independent vs Chasing: $B \pm SE = 0.184 \pm 0.044$, $p < 0.001$). See Figure 4.6.

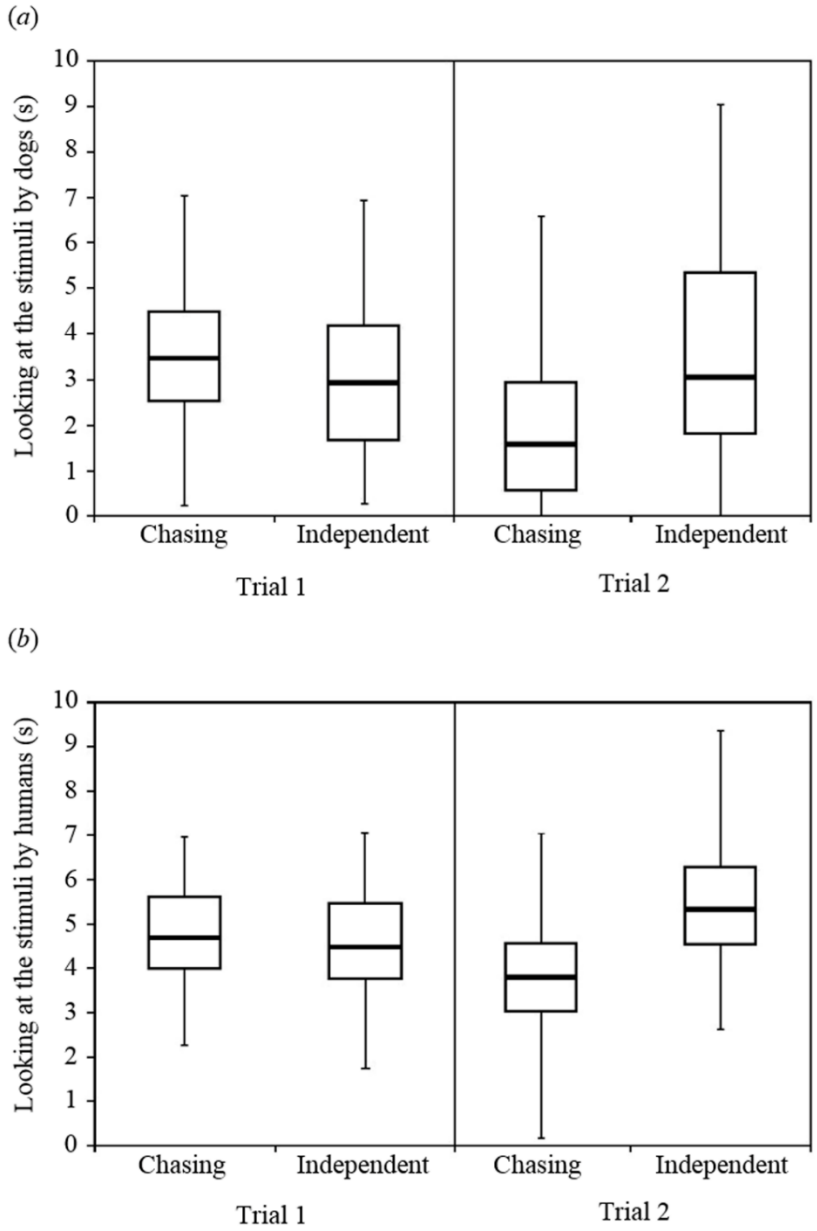


**Figure 4.6.** Duration of looking at the chasing and independent patterns in Trial 1 and 2 by (a) dogs and (b) human participants. The boxplots indicate the median, 25$^{th}$ and 75$^{th}$ percentiles (boxes), and the minimum and maximum (whiskers).

*Within-trial dynamics in looking at stimuli*

Figure 4.7 and 4.8 demonstrates species-differences in looking times at the stimuli (combined, i.e. looking at any of the independent or the chasing pattern). While humans understood the task and watched the stimuli over the whole trial (Trial 1: $B \pm SE = 0.000 \pm 0.001$, $p = 0.846$; Trial 2: $B \pm SE = -0.001 \pm 0.002$, $p = 0.442$), dogs had a greater variability and did not keep a constant focus (Trial 1: $B \pm SE = -0.009 \pm 0.003$, $p < 0.001$; Trial 2: $B \pm SE = -0.006 \pm 0.002$, $p = 0.016$).

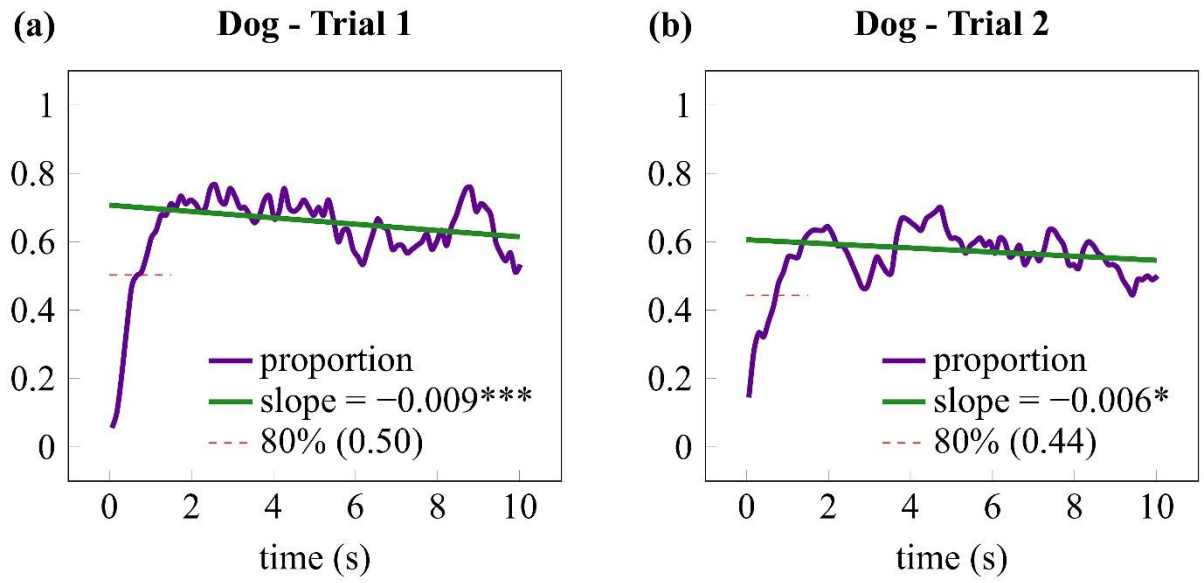


**Figure 4.7.** Proportion of looking at the stimuli in dogs. Regression lines were fitted using data after the proportion values reached the 80 % threshold computed from the average proportion of looking time at stimuli during the trial for the subject. * $p < 0.05$, *** $p < 0.001$.

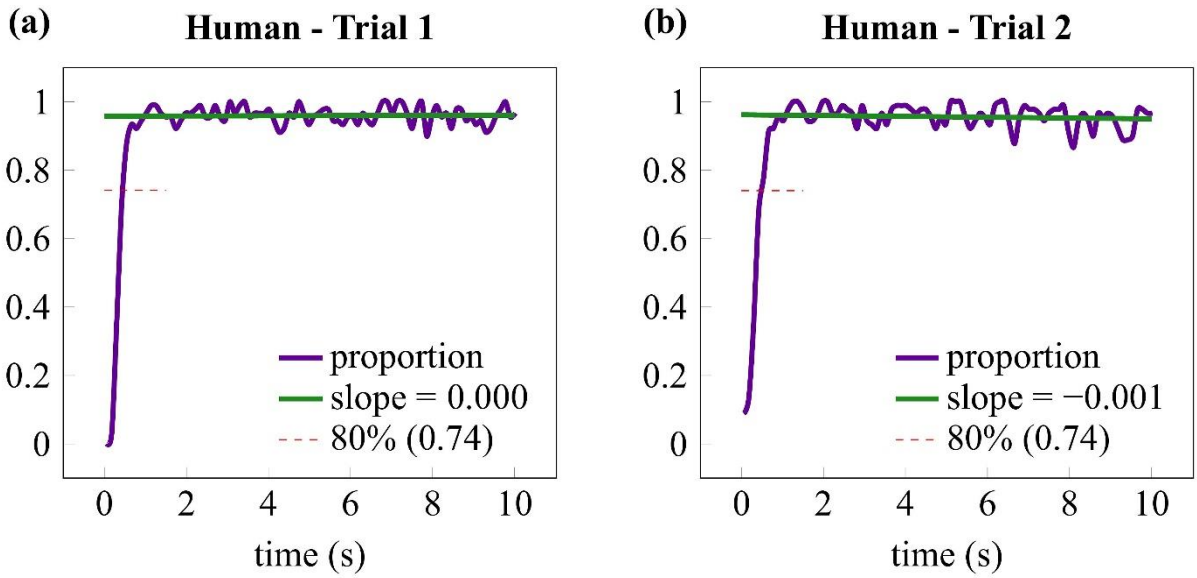


**Figure 4.8.** Proportion of looking at the stimuli in humans. Regression lines were fitted using data after the proportion values reached the 80 % threshold computed from the average proportion of looking time at stimuli during the trial for the subject.

When analysing within-trial dynamics of looking times separately for each movement patterns, we found that dogs' attention to the independent pattern decreased significantly during Trial 1, while they kept their interest for the chasing pattern (Trial 1: Chasing, B ± SE = -0.003 ± 0.003, p = 0.394; Independent, B ± SE = -0.007 ± 0.003, p = 0.017; Figure 4.9). In Trial 2 there was a significant decrease in dogs' looking times for the chasing pattern, while they kept their attention toward the independent pattern (Trial 2: Chasing, B ± SE = -0.008 ± 0.003, p = 0.005; Independent, B ± SE = 0.002 ± 0.003, p = 0.566; Figure 4.9). In humans we found an increasing attention toward the chasing pattern during Trial 1 (Trial 1: Chasing, B ± SE = 0.006 ± 0.003, p = 0.037; Independent, B ± SE = -0.006 ± 0.003, p = 0.066; Figure 4.10). In Trial 2 humans overall looked longer at the independent pattern (see above), but the within-trial dynamics of their looking at stimuli did not change during the trial (Trial 1: Chasing, B ± SE = -0.003 ± 0.003, p = 0.38; Independent, B ± SE = 0.002 ± 0.003, p = 0.600; Figure 4.10).

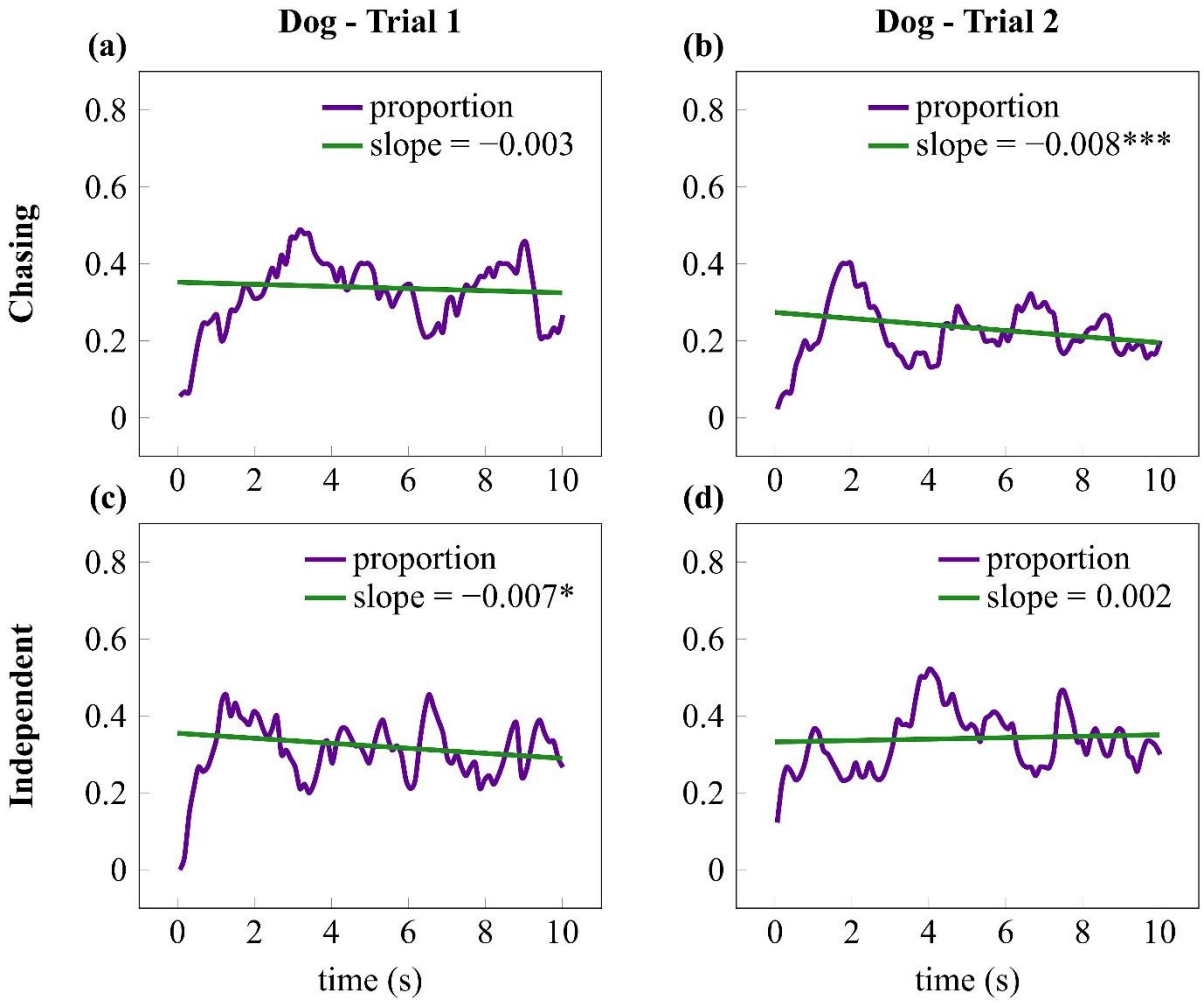


**Figure 4.9.** Proportions of looking at the chasing and the independent stimuli in dogs. Regression lines were fitted using data after the proportion values reached the 80 % threshold computed from the average proportion of looking time at stimuli during the trial for the subject (see Figure 4.7). * $p < 0.05$, *** $p < 0.001$.

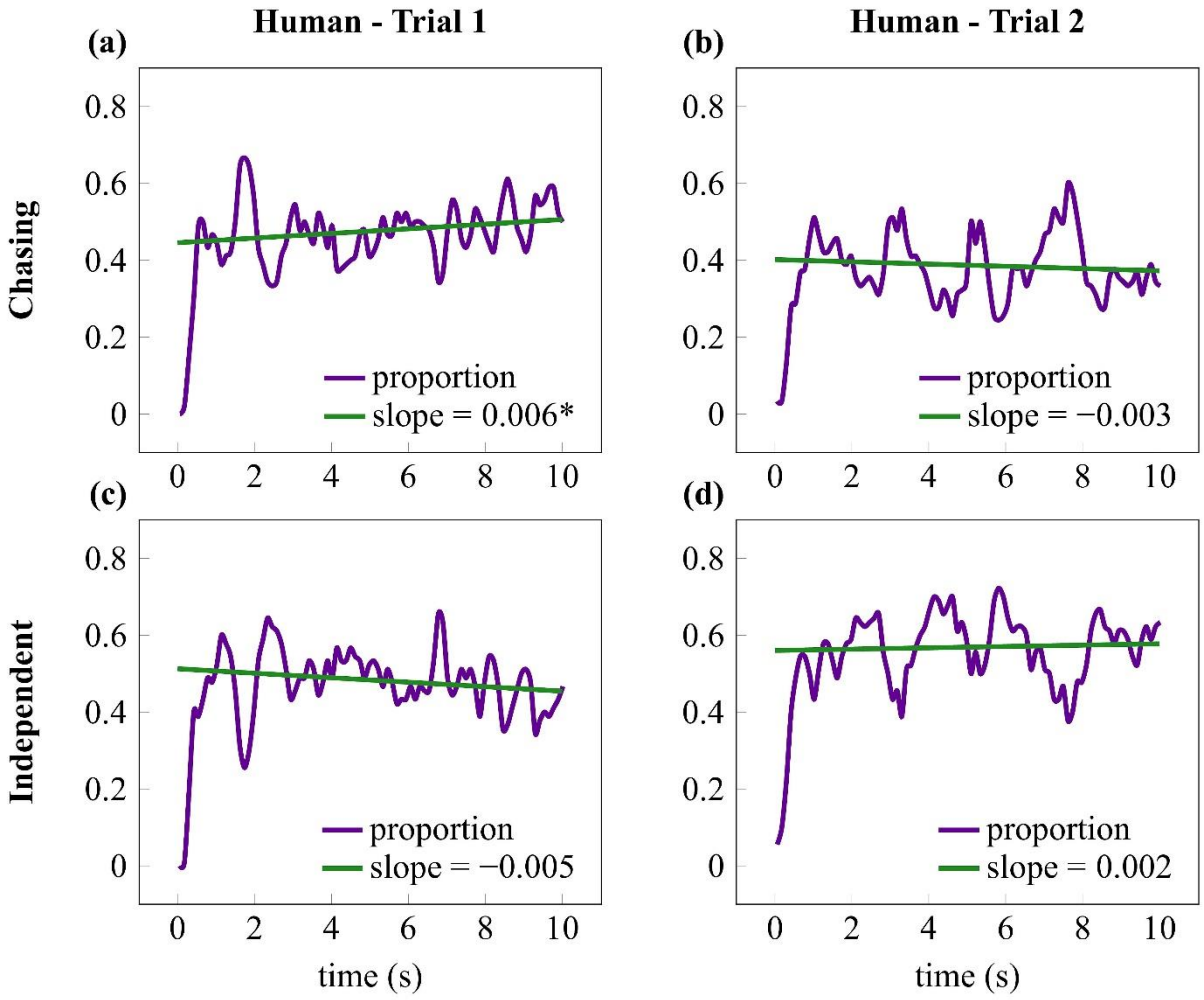


**Figure 4.10.** Proportions of looking at the chasing and the independent stimuli in humans. Regression lines were fitted using data after the proportion values reached the 80 % threshold computed from the average proportion of looking time at stimuli during the trial for the subject (see Figure 4.8). * $p < 0.05$

*Alternation of look between patterns*

We found significant two-way interaction between species and trial, regarding the frequency of change in look between the patterns (loglinear GLMM: *Species x Trial*, $F_{1,116} = 7.721$, $p = 0.006$). In both trials humans changed their look between the chasing and independent patterns more often than dogs (Trial 1: $F_{1,116} = 39.543$, $p < 0.001$; Dogs vs Humans, $B \pm SE = -5.312 \pm 0.845$, $p < 0.001$; Trial 2: $F_{1,116} = 66.629$, $p < 0.001$; Dogs vs Humans $B \pm SE = -5.705 \pm 0.699$, $p < 0.001$). The analysis also revealed that dogs and humans both alternated their look more frequently in Trial 1 than in Trial 2 (Dogs: $F_{1,116} = 19.418$, $p < 0.001$; Trial 1 vs Trial 2, $B \pm SE = 2.032 \pm 0.461$, $p < 0.001$; Humans: $F_{1,116} = 4.713$, $p = 0.032$; Trial 1 vs Trial 2, $B \pm SE = 1.639 \pm 0.755$, $p = 0.032$). See Figure 4.11.

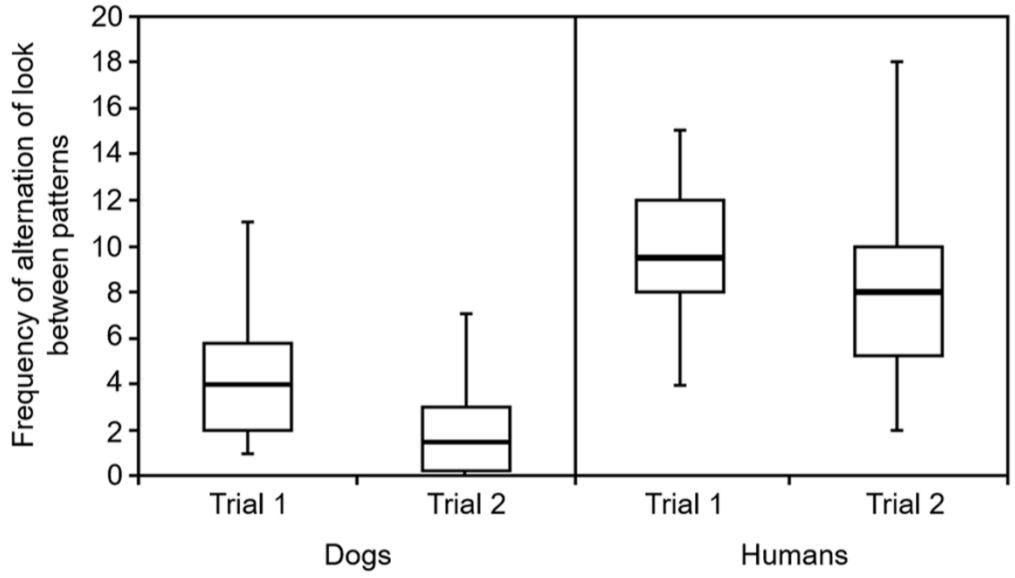


**Figure 4.11.** Frequency of alternating the look between the chasing and independent patterns in Trial 1 and 2 by dogs and human participants. The boxplots indicate the median, 25$^{th}$ and 75$^{th}$ percentiles (boxes), and the minimum and maximum (whiskers).

## 4.1.3. Discussion

These results suggest that dogs and humans showed initial attention to both patterns, but they favoured watching the independent pattern later. Although overall humans looked longer at the projected video than dogs, we found that the two species allocated their attention similarly across the experiment. We suggest that the decreased looking time at the chasing pattern across trials in both species was due to the spontaneous habituation to and/or recognition of the chasing pattern; this could have shifted attention to the independent (unrecognized) pattern. These

results are in line with those reported for five-month-old infants and adults by Rochat et al. (1997), who argued that sensitivity to social causality may explain such a shift in attention.

Although dogs and humans divided their attention similarly between the two patterns, we found a difference in their overall looking time at the screen, and there are further, subtle differences between the two species. Overall decreased look in dogs was the result of decreased look at the independent pattern in the first trial, and decreased look at the chasing pattern in the second trial, suggesting that although their attention weakened, they kept it on the preferred pattern. Considering that many dogs are not used to watching screens (e.g. computer or TV), the differences between the two species regarding within-trial dynamics of their look, are likely not due to dogs' lack of interest in the stimuli, but in projections in general. These results strengthen that both species showed interest in the chasing pattern first and turned their attention toward the independent pattern later.

Although we found that humans change their look between the patterns more often than dogs, it seems that in the present study it did not have an effect on the overall looking times of the two species (for the discussion of species difference regarding this behaviour, see Section 4.2.3).

Behavioural evidence suggests that reduced interobject spacing is an important cue in guiding the attention of adults and children older than a year toward objects (e.g. Meyerhoff et al. 2014a; Galazka and Nyström 2016). In this study, neither dogs nor humans looked more at the chasing pattern in either of the trials, although in humans we measured a slight gradual increase in looking time at the chasing pattern in Trial 1. Considering the overall high proximity of dots in the chasing pattern, we cannot be sure whether increased looking times at the chasing pattern (at least in Trial 1) were due to the specific interaction or reduced interobject spacing. An important difference in experimental setups is that in both previous studies the objects moved with constant speed (Meyerhoff et al. 2014a; Galazka and Nyström 2016), whereas in our stimuli (in both patterns), the objects showed more dynamism with changing speeds. A further source of difference may come from the object's reactions to the changes in the other object's speed, in the case of the chasing pattern.

## 4.2. Importance of directionality in the perception of animacy

The above results suggest not only that dogs perceive animacy, but also that dogs and humans react similarly to these cues; however, we used most motion characteristics that have been described to facilitate the perception (see above). In previous studies, researchers investigated how changing the features of the chasing motion can facilitate (e.g. directionality in the movement of the objects) or prevent (e.g. deviation from heat-seeking chasing) the perception of the pattern (e.g. Tremoulet and Feldman 2000; Szego and Rutherford 2007; Gao et al. 2009; Gao and Scholl 2011; Frankenhuis et al. 2013; Meyerhoff et al. 2013). Here our aim was to investigate whether dogs are also sensitive to such cues, and whether they react similarly to these changes as humans. As a first step, in the present experiment we changed only one aspect of the stimuli. Instead of dots, we used isosceles triangles which provided orientation to the geometric figures that could facilitate the perception of the direction of motion, as well as its exact orientation (heat-seeking pursuit indicated not only by the motion, but the shape as well) (for similar experiment in humans see Tremoulet and Feldman 2000; Gao et al. 2009). We hypothesised that this feature would facilitate the perception, thus compared to the previous findings subjects would shift their attention to the independent motion already in the first trial.

### 4.2.1. Method

#### Constructing stimuli

We displayed the same videos to subjects as in the previous study (Section 3.1); the only difference was that instead of dots we used isosceles triangles circumscribed around the original dots, with *vertex angle 45°* (Figure 4.12).

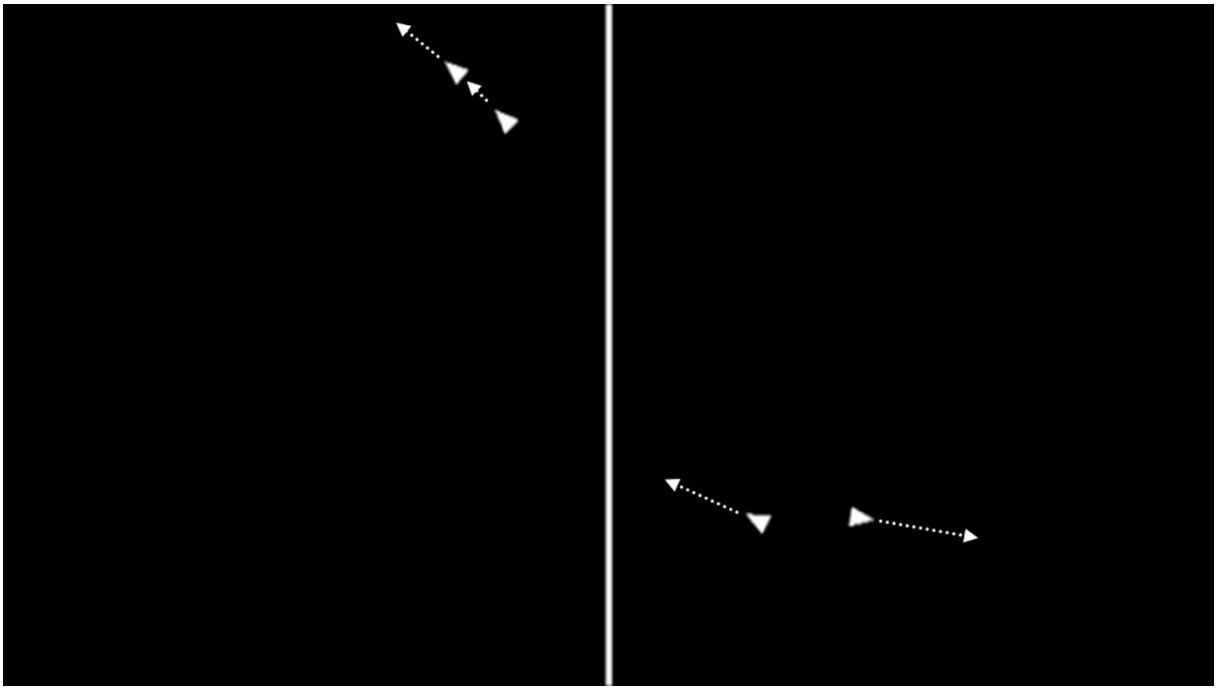

**Figure 4.12.** Snapshot from the displayed video. On the left side of the picture the dots are chasing each other, while on the right side two dots are moving independently from each other. Sides of the chasing and independent patterns are separated by a white vertical line. Dotted arrows show the direction of movement.

## Subjects

*Dogs*

Ethical approval was obtained from the National Animal Experimentation Ethics Committee (PEI/001/1492-4/2015). Owners provided a written consent form to voluntarily permit their dogs to participate in the study. We only tested dogs whose owner did not report any problem regarding the dog's eyesight.

Overall we tested 53 dogs, of them 30 dogs remained in the final analysis (different breeds; 15 females; mean age ± SD 4.1 ± 2.8 years; see Table A4 in Appendix). We excluded eleven dogs due to procedural problems (recording of the test got lost due to a computer problem, the picture of the camera capturing subjects' eyes froze for more than 1 s, the displayed video froze for more than 1 s or the camera could not capture the dog's eyes at all the times), and twelve dogs because they looked at the stimuli for less than 1 s in either of the trials.

Age did not have an effect on dogs' looking times (tested for the overall looking time at the screen, LMM: Age x Trial, $F_{1,27} = 0.411$, $p = 0.527$; Age, $F_{1,27} = 0.010$, $p = 0.922$). We only tested dogs whose owner did not report any problem regarding the dog's eyesight.

*Humans*

Ethical approval was obtained from the Institutional Psychological Ethics in Research Committee (EPKEB-2017/13). Participants (all of legal age) provided a written consent form that they participate in the study voluntarily. All participants had normal or corrected to normal vision.

We tested 32 university students; we had to exclude two participants due to the quality of the recording. Thus in the final analysis we had 30 human participants (22 females; mean age ± SD 21.7 ± 1.2 years; see Table A5 in Appendix).

## Apparatus

We used the same apparatus as in the previous study (Chapter 3.1).

## Procedure

The procedure was the same as in the previous study (Chapter 3.1); the only difference was the use of triangles as moving figures instead of dots (see above).

## Data analysis

All tests were recorded and subjects' behaviour was analysed with Solomon Coder 17.03.22; videos were coded frame-by-frame (25 fps). We coded the looking direction of subject (chasing, independent or away) for each frame based on their eye movements.

We used looking duration (s) as explained variables in statistical analysis. In dogs, the looking duration toward the stimuli in both trials were normally distributed according to the visual inspection of the Q-Q plots and based on the Kolmogorov-Smirnov tests (Trial 1: Chasing $D_{30} = 0.079$, $p > 0.200$; Independent $D_{30} = 0.123$, $p > 0.200$; Trial 2: Chasing $D_{30} = 0.131$, $p > 0.200$; Independent $D_{30} = 0.088$, $p > 0.200$). Looking duration of humans was also normally distributed according the visual inspection of the Q-Q plots and also based on the Kolmogorov-Smirnov tests (Trial 1: Chasing $D_{30} = 0.119$, $p > 0.200$; Independent $D_{30} = 0.083$, $p > 0.200$; Trial 2: Chasing $D_{30} = 0.094$, $p > 0.200$; Independent $D_{30} = 0.075$, $p > 0.200$).

Statistical analysis was conducted using IBM SPSS Statistics 22. We used linear Generalized Linear Mixed Model (GLMM) (adjusted with sequential Sidak) to analyse the effects of motion pattern (*chasing* and *independent*), trial (*Trial 1* and *2*) and species (*dog* and *human*) on looking time. For significant explanatory variables, we provide parameter estimates (B ± SE).

We conducted the same analysis as in the previous study to investigate within-trial dynamics of looking at the stimuli.

We further analysed the frequency of changing the look between the two motion patterns by counting the number of change *from chasing to independent* and *from independent to chasing* (irrespectively of whether there was a delay in between). Based on the AIC values, we used loglinear GLMM for the analysis, because data fit best the Poisson distribution (model with the lowest AIC value was kept, we considered a model better whenever delta AIC was $\geq 2$; AIC = 175.386). For significant explanatory variables, we provide parameter estimates ($B \pm SE$).

Inter-coder reliabilities were investigated on random subsamples of the recordings (dogs: Attila Lengyel, humans: Judit Abdai), coders repeatedly coded 20 % of dog and 20 % of human subjects. We exported the full coding sheets of both coders from the Solomon Coder and checked the correspondence between the coders for all data points (i.e. about 500 data point pairs regarding the frame-by-frame coding of the videos recorded in 25 fps). We analysed the consensus between coders calculating Cohen's kappas (average ± SD Cohen kappas, dogs: 0.820 ± 0.082; humans 0.789 ± 0.149).

### 4.2.2. Results

We found significant three-way interaction between species, trial and pattern (linear GLMM of looking times: *Species x Trial x Pattern,* $F_{1,232} = 6.418$, $p = 0.012$; for detailed results see Table 4.2). Dogs looking duration toward the two patterns were different both in Trial 1 and 2. In Trial 1 they looked longer at the chasing, while in Trial 2 the independent pattern. Looking times at the patterns in humans were marginally different in Trial 1, but we found significant difference in Trial 2. Although humans looked only marginally longer the independent pattern in Trial 1, in Trial 2 they looked at it significantly longer. The analysis also showed difference between the two species in Trial 1 regarding the independent pattern, and in Trial 2 regarding the chasing pattern; however, there was no difference between species in Trial 1 regarding the chasing, or in Trial 2 regarding the independent pattern. In Trial 1 human participants looked longer at the independent pattern than dogs did, and in Trial 2 humans also looked longer at the chasing pattern than dogs. Based on the three-way interaction, we also showed that while in humans there is no difference in looking at either of the patterns between trials, dogs looking times at the chasing pattern were different between trials, but only marginally different in case of the independent pattern. Dogs looked at the chasing pattern less in Trial 2, than in Trial 1, and looked marginally longer the independent pattern in Trial 2 than in Trial 1. See Figure 4.13.

**Table 4.2.** Effect of *species*, *trial* and *pattern* on subjects' looking times (linear GLMM). For significant explanatory variables in the final models, we provide contrast estimates (B ± SE) and *t* values (significant variables are indicated with orange background, marginally significant variables are indicated with grey background). *X vs Y* means that the behaviour was more/less emphasized in case of *X* compared to *Y* (e.g. positive B ± SE in case of Chasing vs Independent means that subjects looked longer at the chasing compared to the independent pattern).

| **Species** | **Trial** | **Pattern** | **F value ($df_1$=1, $df_2$=232)** | **B ± SE** | ***t* value (df=232)** | **p value** |
|---|---|---|---|---|---|---|
| ***Between pattern*** | | | | | | |
| **Dog** | **1** | **Chasing vs Independent** | 4.604 | 0.952 ± 0.444 | 2.146 | = 0.033 |
| | **2** | | 20.457 | -2.007 ± 0.444 | -4.523 | < 0.001 |
| **Human** | **1** | | 3.642 | -0.847 ± 0.444 | -1.908 | = 0.058 |
| | **2** | | 12.231 | -1.557 ± 0.444 | -3.510 | = 0.001 |
| ***Between species*** | | | | | | |
| **Dog vs Human** | **1** | **Chasing** | 1.601 | - | - | = 0.207 |
| | | **Independent** | 7.778 | -1.237 ± 0.444 | -2.789 | = 0.006 |
| | **2** | **Chasing** | 6.028 | -1.089 ± 0.444 | -2.455 | = 0.015 |
| | | **Independent** | 2.081 | - | - | = 0.151 |
| ***Between trials*** | | | | | | |
| **Dog** | **1 vs 2** | **Chasing** | 22.120 | 2.087 ± 0.444 | 4.703 | < 0.001 |
| **Human** | | | 0.966 | - | - | = 0.327 |
| **Dog** | | **Independent** | 3.863 | -0.872 ± 0.444 | -1.965 | = 0.051 |
| **Human** | | | 0.383 | - | - | = 0.536 |

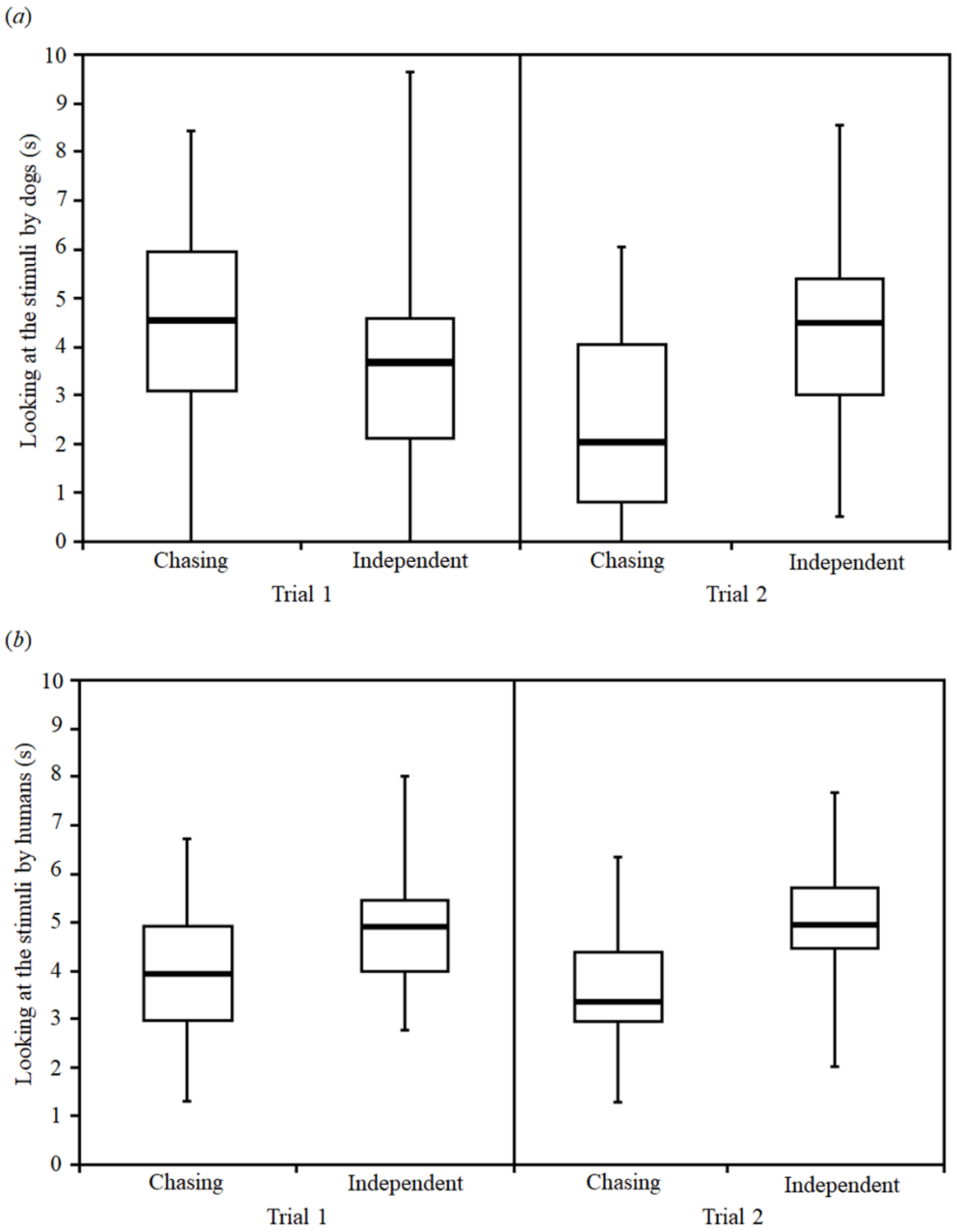


**Figure 4.13.** Duration of looking at the chasing and independent patterns in Trial 1 and 2 by (a) dogs and (b) human participants. The boxplots indicate the median, 25$^{th}$ and 75$^{th}$ percentiles (boxes), and the minimum and maximum (whiskers).

*Within-trial dynamics in looking at stimuli*

Figure 4.14 and 4.15 shows the looking times of the two species toward the stimuli (at the independent and chasing patterns combined). While dogs in Trial 1 watched the stimuli constantly, in Trial 2 their looking duration decreased toward it (Trial 1: ±± SE = 0.003 ± 0.002, p = 0.148; Trial 2: B ± SE = -0.014 ± 0.002, p < 0.001). Compared to the previous study in which humans kept a constant focus, here we found that their looking duration increased during Trial 1, but there was no change in Trial 2 (Trial 1: B ± SE = 0.007 ± 0.002, p < 0.001; Trial 2: B ± SE = -0.002 ± 0.002, p = 0.372).

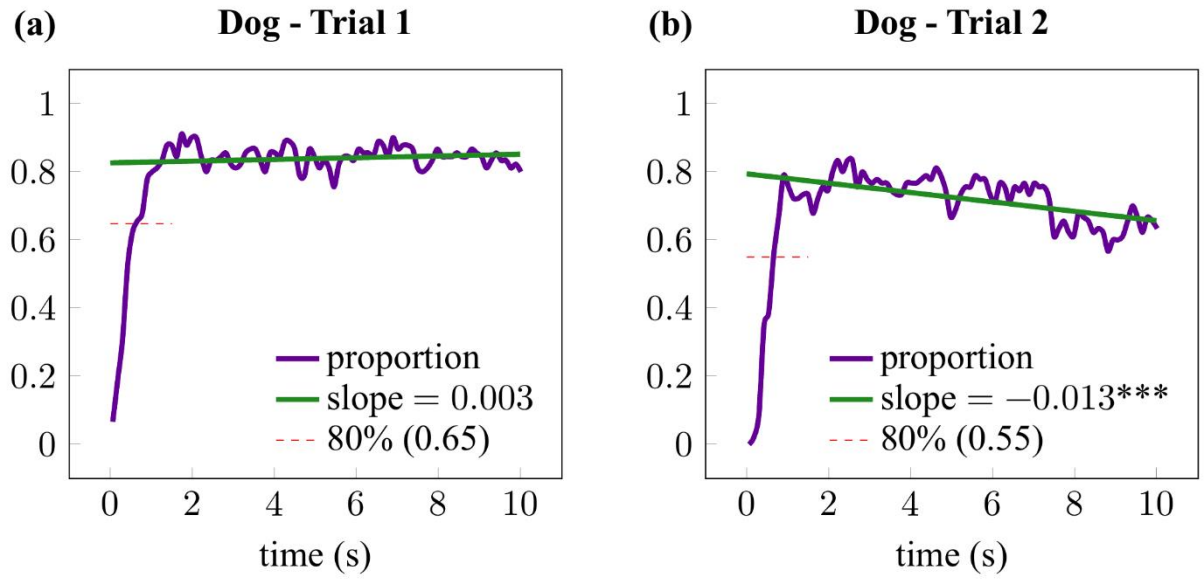


**Figure 4.14.** Proportion of looking at the stimuli in dogs. Regression lines were fitted using data after the proportion values reached the 80 % threshold computed from the average proportion of looking time at stimuli during the trial for the subject. *** p < 0.001

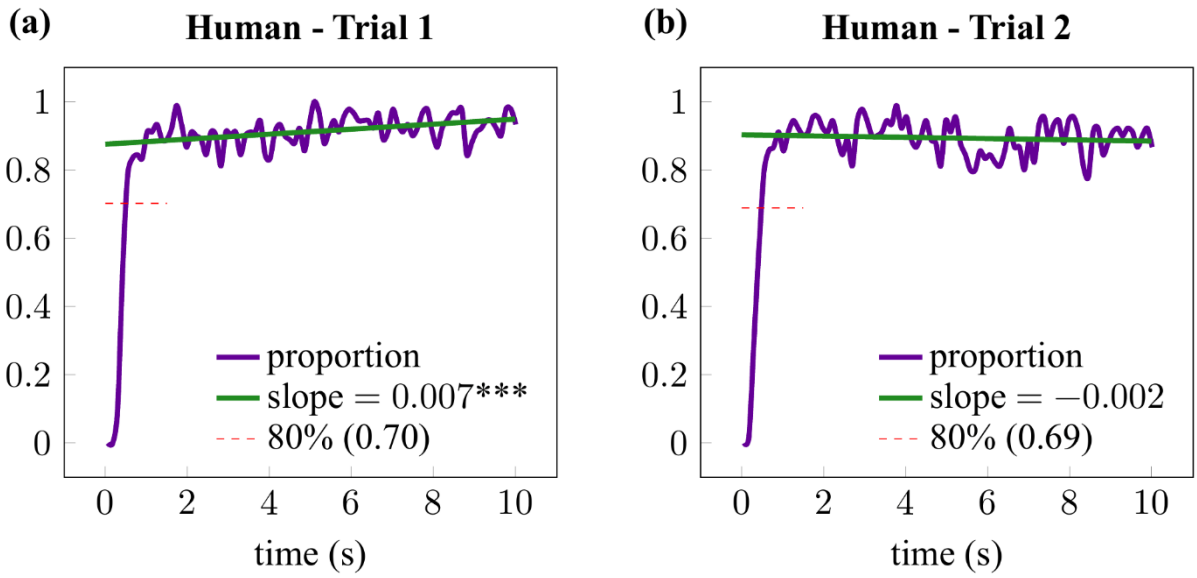


**Figure 4.15.** Proportion of looking at the stimuli in humans. Regression lines were fitted using data after the proportion values reached the 80 % threshold computed from the average proportion of looking time at stimuli during the trial for the subject. *** $p < 0.001$

We further analysed subjects' looking duration toward each movement patterns separately. It revealed that dogs in Trial 1 increased their attention toward the chasing pattern, while it decreased toward the independent pattern (Dogs, Trial 1: Chasing, $B \pm SE = 0.012 \pm 0.002$, $p < 0.001$; Independent, $B \pm SE = -0.009 \pm 0.002$, $p < 0.001$; Figure 4.16). Dogs overall decreased attention toward the stimuli in Trial 2 was driven by decreased looking time at the chasing pattern, while their looking time at the independent pattern did not change (Dogs, Trial 2: Chasing, $B \pm SE = -0.011 \pm 0.002$, $p < 0.001$; Independent, $B \pm SE = -0.003 \pm 0.002$, $p = 0.154$; Figure 4.16). We found the opposite change in looking time in humans during Trial 1; participants' looking time decreased toward the chasing, while increased toward the independent pattern (Humans, Trial 1: Chasing, $B \pm SE = -0.017 \pm 0.004$, $p < 0.001$; Independent, $B \pm SE = 0.025 \pm 0.004$, $p < 0.001$; Figure 4.17). However, in Trial 2 there was no change in their attention to either of the patterns (Humans, Trial 2: Chasing, $B \pm SE = 0.003 \pm 0.002$, $p = 0.238$; Independent, $B \pm SE = -0.005 \pm 0.003$, $p = 0.130$; Figure 4.17).

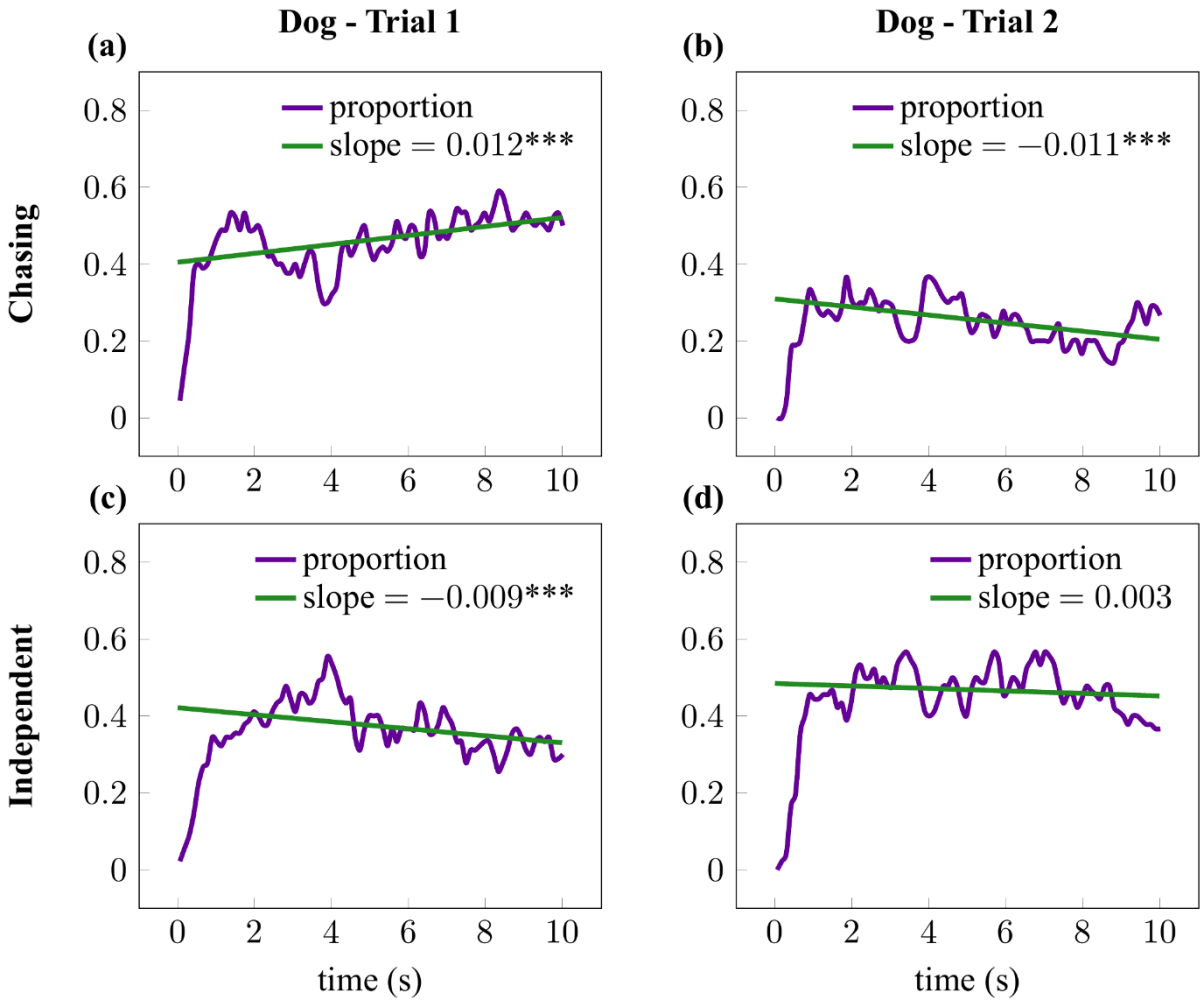


**Figure 4.16.** Proportions of looking at the chasing and the independent stimuli in dogs. Regression lines were fitted using data after the proportion values reached the 80 % threshold computed from the average proportion of looking time at stimuli during the trial for the subject (see Figure 4.14). *** $p < 0.001$

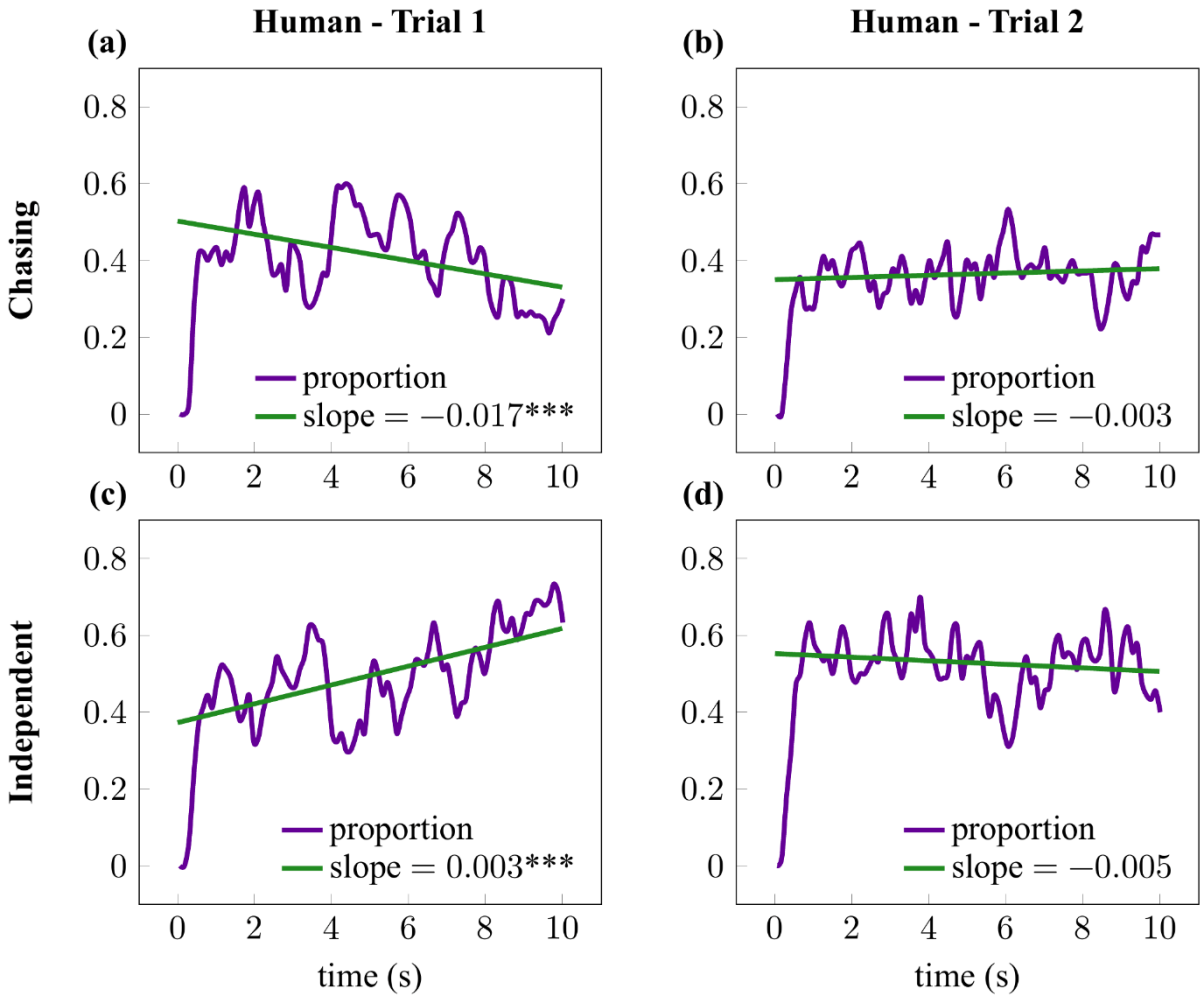


**Figure 4.17.** Proportions of looking at the chasing and the independent stimuli in humans. Regression lines were fitted using data after the proportion values reached the 80 % threshold computed from the average proportion of looking time at stimuli during the trial for the subject (see Figure 4.15). *** $p < 0.001$

*Alternation of look between patterns*

We found significant two-way interaction between species and trial, regarding the frequency of change in look between the patterns (loglinear GLMM: *Species x Trial*, $F_{1,116} = 4.077$, $p = 0.046$). In both trials humans changed their look between the chasing and independent patterns more often than dogs (Trial 1: $F_{1,116} = 18.073$, $p < 0.001$; Dogs vs Humans, $B \pm SE = -3.389 \pm 0.797$, $p < 0.001$; Trial 2: $F_{1,116} = 35.378$, $p < 0.001$; Dogs vs Humans $B \pm SE = -4.135 \pm 0.695$, $p < 0.001$). The analysis also revealed that dogs alternated their look more frequently in Trial 1 than in Trial 2 (Dogs: $F_{1,116} = 10.609$, $p = 0.001$; Trial 1 vs Trial 2, $B \pm SE = 1.597 \pm 0.490$, $p = 0.001$); however, in humans there was no difference between trials (Humans: $F_{1,116} = 1.502$, $p = 0.223$). See Figure 4.18.

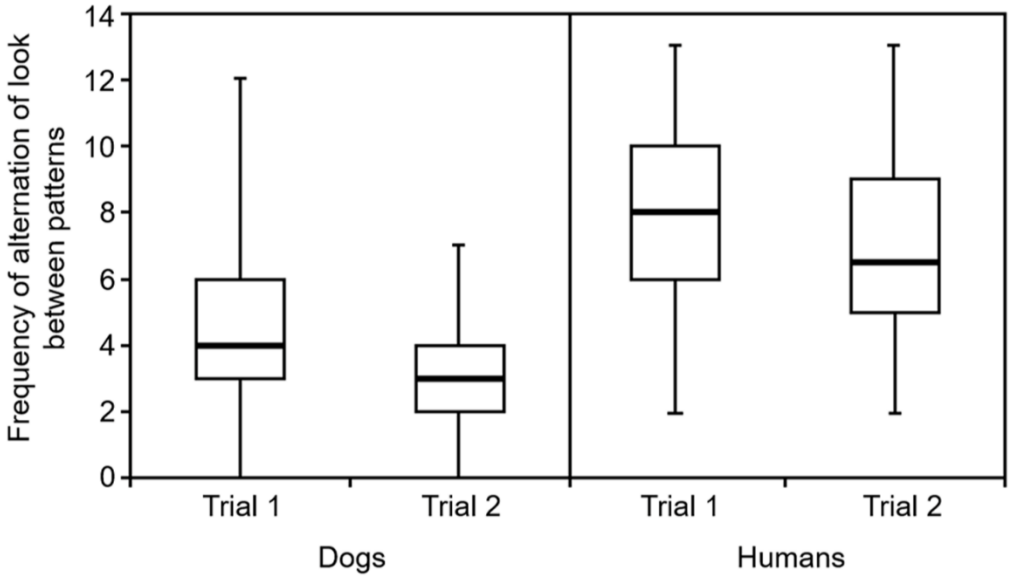


**Figure 4.18.** Frequency of alternating the look between the chasing and independent patterns in Trial 1 and 2 by dogs and human participants. The boxplots indicate the median, 25$^{th}$ and 75$^{th}$ percentiles (boxes), and the minimum and maximum (whiskers).

### 4.2.3. Discussion

Compared to our previous findings using dots as moving objects [4], we found change in the initial behaviour of both species. Results suggest that similarly as in the previous study, spontaneous recognition of the chasing pattern led to increased attention to the independent pattern (suggesting animacy perception). But while humans increased their look to the independent motion gradually from the start of the first trial, dogs initially increased their look to the chasing pattern, and started to focus their attention to the independent pattern only later. This result confirms at least in case of humans, that interobject spacing is not likely to draw attention to the chasing pattern in this context (cf. Meyerhoff et al. 2014a; Galazka and Nyström 2016).

Considering that previously in humans increasing attention to the chasing pattern was found during the first trial, the change in looking preference is important here. However, dogs seemed to keep their attention on the chasing pattern (while decreasing it toward the independent motion) in the previous study, meaning that adding orientation to the moving objects only enhanced this difference.

We propose that differences in the behaviour of dogs and humans are the result of the difference in the frequency of alternation of look between patterns. Dogs fixate their look longer on the preferred pattern (chasing in Trial 1 and independent motion in Trial 2), while humans change their look between them more often. Morphological, physiological as well as ecological differences can explain the difference in the behaviour of dogs and humans. Related to the structure of the skull, we propose that the difference between dogs and humans may originate from the difference of the position of eyes. The width of the visual field of dogs can reach 250°; further the angle of the field of best vision is larger in dogs, than in humans (5° and 0.5-0.7°, respectively) (Sherman and Wilson 1975; Miller and Murphy 1995; Heffner and Heffner 2003). Also, in dogs the distribution of cones and ganglion cells is elongated (visual streak; cf. fovea in primates), providing better vision in a narrow horizontal strip (Peichl 1992; Mowat et al. 2008). Breed differences have also been described regarding the expression of the temporal arm of the streak (see e.g. Peichl 1992). For example, in a recent study Bognár et al. (2018) tested looking times of dogs toward projected images of dog and human faces, and they found breed differences based on skull length. Based on this, dogs may need less movement to be able to see both patterns while humans have to change their look between them in order to assess both patterns properly.

Rochat et al. (1997) found that five-month-old infants switch their looks more often between a chasing and independent motion pattern than three-month-olds. They argued that older infants

are more engaged in comparing the patterns. However, we suggest that there can be a difference between the processing of the visual stimuli between the age groups which causes this difference. For example, Helo et al. (2016) found that duration of fixation on visual scenes decrease from three to twelve months of age in infants; however, between three to nine months of age there seems to be no difference among age groups. Thus it is still an open question whether such explanation may account for the results of Rochat and colleagues (1997).

Evolutionary constraints should be considered here as well. Humans had to adapt to a dynamic and always changing environment, thus they need to actively explore their surrounding; for this they need to change the focus of the eye frequently (Hoppe and Rothkopf 2016). Hoppe and Rothkopf (2016) found that humans rapidly adjust the temporal eye movement to the regularity of changes in the surrounding. For predators focusing the eye on the prey is crucial during pursuit, while individuals need to check for changes in the environment less frequently. This difference may explain the difference between the alternation of look between dogs and humans. This is only a hypothetical scenario, but we suggest that this would be an intriguing future research area.

## 4.3. Novel approach to study animacy perception in non-human species

In the above experiments we used video projection to study animacy perception which allowed us to compare the results with studies previously conducted with human infants, and also facilitate the systematic change in parameters of the pattern. One important issue in comparative studies however, is that similar tasks may not be appropriate to test the same (or similar) phenomenon in different species. The method applied by Rochat et al. (1997) seems to be a great approach to study visual perception (cf. Goto et al. 2002; Atsumi and Nagasaka 2015 in which prior training was applied). However, contrary to humans, non-human species are not used to watching screens that may interfere with the investigated question (but see in dogs e.g. Pongrácz et al. 2003; Péter et al. 2013). Thus here we designed a novel method to study perception of animacy in non-human species, which we have tested in dogs. We presented the chasing and independent motion patterns in live demonstration by using moving inanimate agents (UMOs – Unidentified Moving Objects). UMOs have been used successfully in previous studies as interactive partners to investigate social behaviour of dogs (e.g. Gergely et al. 2013, 2016; Abdai et al. 2015). Across studies we found that dogs are willing to interact with UMOs

and comprehend on their visual signals in various situations (Gergely et al. 2013, 2015), and the interactive UMO was able to elicit counterproductive choice in dogs (Abdai et al. 2015; Gergely et al. 2016); but only when it showed social-like behaviour. We hypothesised that compared to the relatively complex behaviour used in these studies (e.g. communicative behaviour similar to human signalling; Gergely et al. 2015), dogs might also discriminate between inanimate agents (animate- vs inanimate-like agents) when only specific motion cues are available. Thus we expected that dogs would discriminate between UMOs involved in the chasing compared to the independent motion pattern, and thus they would show more interest (or initiate interaction) with the UMOs that participated in the demonstration of the chasing pattern, rather than the other UMOs.

### 4.3.1. Method

#### Subjects

Ethical approval was obtained from the National Animal Experimentation Ethics Committee (PE/EA/2484-4/2016). Owners provided a written consent form to voluntarily permit their dogs to participate in the study.

Overall we tested 35 dogs that have not had previous experience with UMOs. We excluded eleven dogs: one dog due to technical difficulties with one of the UMOs during the *Observation phase*; two dogs, because they showed distress in the presence of the UMOs; one dog was influenced by the owner during the *Test phase*; one dog looked one of the demonstrations less, than 20% of the length of the demonstration; three dogs, because they did not approach any of the UMOs during the *Test phase*; and three dogs due to procedural problem (either the UMOs crashed into each other, or they crashed into the obstacles more than two times by moving them at least 0.5 m away from their original locations; both of these could be salient cues affecting dogs' behaviour toward the agents later). The remaining 24 dogs were from different breeds (15 females; mean age ± SD 4.96 ± 2.99 year; see Table A6 in Appendix).

#### Apparatus

Dogs were tested in a 6.27 m x 5.40 m test room at the Department of Ethology, Eötvös Loránd University (for the full experimental set up see Figure 4.19). Five identical brown pots were placed in the room upside-down serving as obstacles during the demonstration of the movement patterns. During the observation dogs were sitting on a wooden platform covered

with artificial grass (H x W x L: 25 cm x 80 cm x 80 cm), in the middle next to one of the walls. The platform was on a green PVC mat to make it more stable and prevent the slipping. The platform helped dogs' view to the room and separated them physically from the interacting UMOs during the observation phase. The first seven dogs were tested with a smaller and less stable platform (25 cm x 55 cm x 55 cm). We compared the looking duration during the demonstrations between the seven dogs tested with the smaller platform and the first seven dogs that have been tested with the larger platform. Based on the data analysis the differences between the platforms had no effect on dogs' behaviour (independent samples Mann-Whitney U test: Looking at the chasing demonstration, U = 24, p = 1.000; Looking at the independent demonstration, U = 19, p = 0.535); thus we included these dogs into the final analysis as well.

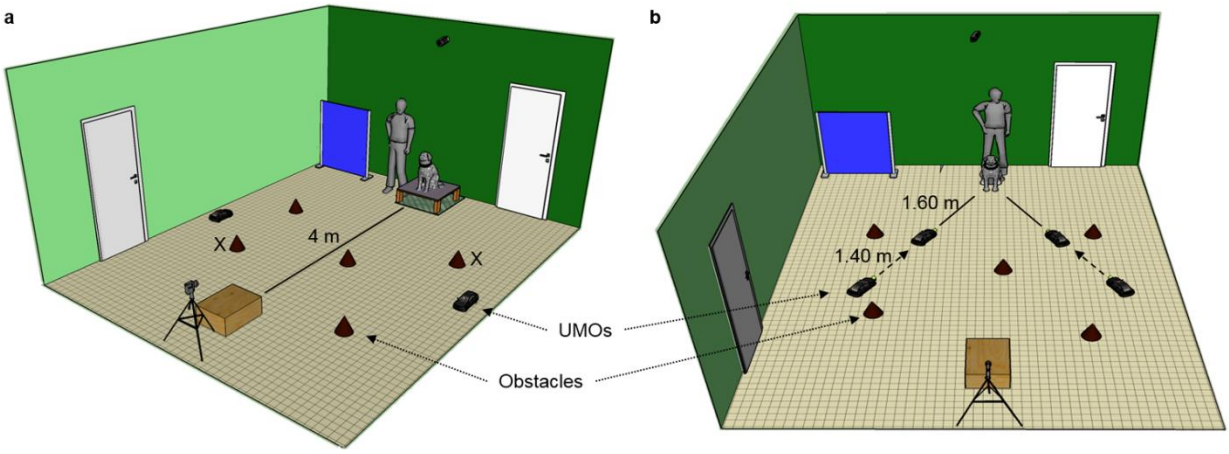


**Figure 4.19.** Experimental set up in the (a) Observation phase (b) Test phase. Dashed arrows indicate the movement of the UMOs toward the dog; X marks indicate the starting points of the chasing and independent patterns.

In front of the dog, next to the opposite wall, we placed a wooden box (38 cm x 48 cm x 80 cm) with a front opening (20 cm x 20 cm) facing to the dog. In the corner on the right side of the dog there was a blue cartonplast occluder (1.27 m x 5.40 m) that was used to cover dogs' view to the room when required.

In the test phase we used two tennis balls that we put on two plastic plates (8 cm × 8 cm) which had metal sheets on their sides. All embodiments of the UMOs were equipped with magnets on their fronts. The plates (containing the balls) could be moved by attaching them to the magnets by the metal sheets.

Tests were recorded by three cameras: one hand camera (Sanyo Xacti) mounted on a tripod behind the box oriented toward the dog, and two fish-eye optic cameras (Mobius ActionCam) synchronised with each other hanging from the ceiling above the dog and the wooden box.

*Inanimate agents (UMOs)*

Two remote-controlled cars were used as UMOs (#32710 RTR Switch Abarth 500, 28 cm x 16 cm x 13 cm; and #7304 Traxxas Ford Mustang Boss 302; 31 cm x 18 cm x 11.5 cm). The UMOs were controlled by Experimenter (E) 1 and E2 from outside through the fish-eye optic cameras. Both UMOs had two different embodiments in colour and shape (one for the demonstration of the chasing pattern and one for demonstrating the independent motion pattern; Figure 4.20). In the following we refer to the remote-controlled cars as UMO 1 and UMO 2 based on the body of the car itself (independently from the embodiment).

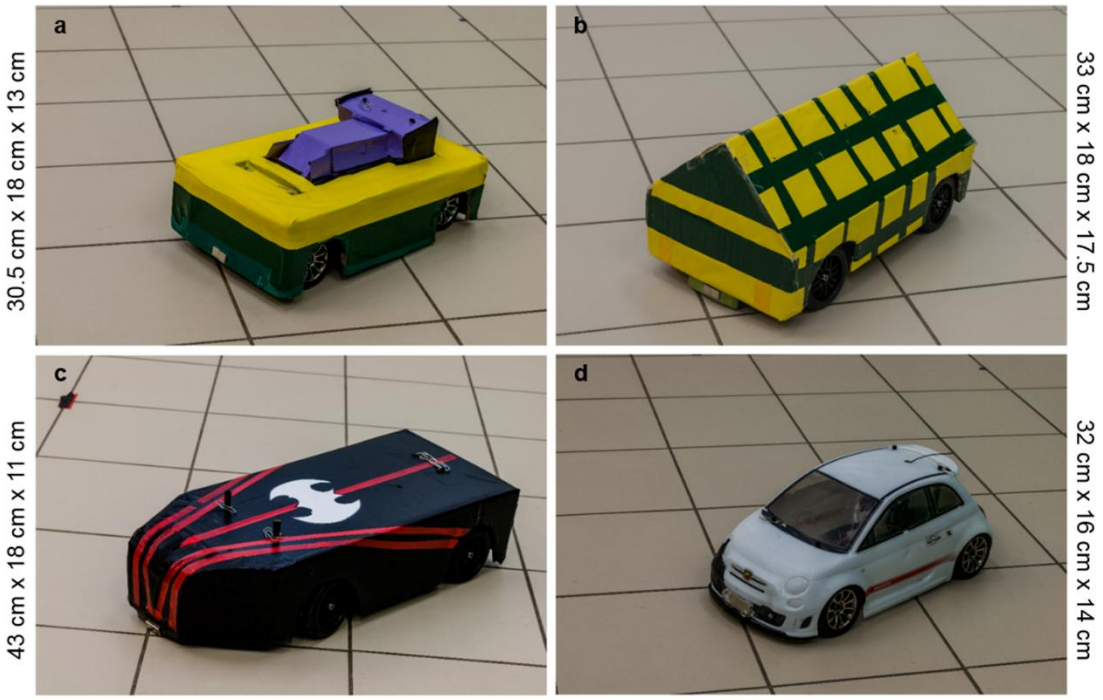


**Figure 4.20.** Embodiments of the UMOs. The (a) and (d) are the embodiments of UMO 1; and (b) and (c) are the embodiments of UMO 2. We used (b) and (d) for the independent demonstration, and (a) and (c) for the chasing demonstration. In the Test phase we had two pairs: (a) and (b); (c) and (d).

### Design of the movement patterns

In the design of the chasing pattern we took into consideration motion characteristics that have been found as important to recognize a chasing pattern in former studies (e.g. Gao et al. 2009; Gao and Scholl 2011; Frankenhuis et al. 2013): (1) the chaser UMO moved directly toward the chased UMO following the shortest route (e.g. if the chased UMO went around an obstacle, the chaser UMO cut the turn and moved directly toward the chased UMO); (2) the chaser UMO oriented toward the chased UMO; (3) the chased UMO executed frequent directional changes during escape; and (4) both UMOs displayed sudden changes in their speed (e.g. when the chaser UMO came within ca. 1 m the chased UMO accelerated). The route was designed in a way that the UMOs spend equal time in the two parts of the room in order to avoid asymmetrical cues.

In case of the independent pattern, both UMOs followed different routes and moved independently from each other. For the design of these routes we gave numbers to the five obstacles and generated a random sequence with numbers from 1 to 5 (CarChase program developed by Bence Ferdinandy). This sequence gave the order of the obstacles that should be passed by (the starting points of the demonstrations were fixed; see Figure 4.19). For the two UMOs that participated in the independent demonstration we generated separate sequences, the number of elements of the sequences was given based on the chasing pattern (how many obstacles the UMOs passed by during this). The program generated the sequence in a way that the UMOs spend equal time in the two parts of the room to avoid asymmetrical cues. At some points of their routes (depending on certain constraints, such as the avoidance of sudden collision) the UMOs increased and decreased their speed, they crossed each other's path, and several times followed the same route right after each other (with a larger distance as in case of the chasing), in order to reduce the difference between the chasing and the independent demonstrations (we aimed to counterbalance the number of these events between the demonstrations). There was no difference in the number of accelerations and sharp direction changes between the two demonstrations (paired-samples t test: Acceleration, $t_{23} = -1.457$, $p = 0.159$; Direction change, $t_{23} = 1.748$, $p = 0.094$; see Table 4.3).

**Table 4.3. Quantitative information on the movement of the UMOs in the chasing and independent demonstrations.**

| | Chasing | Independent |
|---|---|---|
| **Average number of accelerations (± SD)** | 19.83 (± 3.41) | 19.21 (± 3.68) |
| **Average number of sharp direction changes (ca. > 110°) (± SD)** | 11.5 (± 2.90) | 11.96 ± (2.69) |

Due to technical reasons we used only one predetermined route for the chasing, and one for the independent movement pattern. In another study we have found that dogs discriminate between a chasing and an independent movement pattern performed by geometric shapes, when using video displays (Abdai et al. 2017b). Considering that in that study we used different chasing patterns (15 different chasing patterns generated with the same parameters) and did not find any influence of the displayed route itself, we suggest that probably it was not necessary to use multiple different routes in the present study. The experimenters controlled the same UMOs in all the phases and tests (E1 – UMO 1 and E2 – UMO 2). The roles of the UMOs were not interchangeable due to technical reasons; UMO 1 was always the chaser and UMO 2 the chasee in the chasing pattern; UMO 1 was going inside the box during the independent pattern and UMO 2 in the chasing (see the *Procedure*).

## Procedure

*Observation phase*

After the owner and the dog entered the room, the dog explored the room while E1 informed the owner about the procedure. The dog sat on the platform orienting toward the box, the owner stood/sat next to the dog while holding it on a leash. E1 put the occluder in front of the dog while E2 placed the UMOs next to the middle of the walls, on the sides of the dog (Figure 4.19a). In case of the chasing demonstration UMO 2, in case of the independent demonstration UMO 1 was on the left side. E1 removed the occluder and the experimenters left the room. Throughout the test the experimenters used the door next to the dog, the owner with the dog used the other door (Figure 4.19).

Both patterns started with a familiarization during which the UMOs moved simultaneously around the room (elliptical route; different initial positions). After 1.5 rounds the UMOs started to follow their predetermined route by turning away from the elliptical routes at the starting

points which were the same in case of the chasing and independent demonstrations (see Figure 4.19a). Both observation trials ended with one of the UMOs going inside the box (see above) (mean time of the demonstration (s) ± SD, chasing: 71.06 ± 8.21; independent: 94.76 ± 4.24; the longer duration in case of the independent motion trial occurred probably because if the UMOs were too close to each other when UMO 1 went into the box, UMO 2 made an extra round to avoid any motion cues that could have been perceived as an interaction among them). After the first observation trial ended, the dog and the owner left the room. The dog was not allowed to go to the UMOs. E1 and E2 changed the embodiments of the UMOs. The owner and the dog re-entered the room, they went back to their original location and the test was continued with the second observation trial. At the end of this trial the owner and the dog left the room again.

All subjects observed both the chasing and independent patterns. We counterbalanced for the order of the movement patterns between subjects.

*Test phase*

Before the owner and the dog came back, E1 and E2 put away the platform. They changed the embodiment of one of the UMOs, thus one of the UMOs had the embodiment from the independent, while the other had the embodiment from the chasing demonstration. Due to the different sizes of the cars we could only use two combinations (pairs) of the embodiments (Figure 4.20). The used pairs were counterbalanced between subjects.

The owner held the dog at its original position (without the platform); E1 put the occluder in front of the dog and informed the owner about the test phase, while E2 placed the UMOs to their predetermined location, 3 m away from the dog each (Figure 4.19b). E2 brought in two balls and two small plates and stood in front of the dog, in a 1.5 m distance to the middle. E1 removed the occluder and took one of the balls and plates from E2 invisibly to the dog. E1 and E2 stood next to each other, hiding the balls and plates behind their backs. E1 and E2 simultaneously called the dog's attention by saying its name and showed the balls to the dog while putting them on the plates. They attached the plates to the UMOs. If the dog focused only on one of the UMOs, the experimenters gave a non-social signal to the dog (both of them knocked on the floor with their hands in front of the UMOs, without eye-contact). E1 and E2 showed their empty hands to the dog and left the room. The UMOs moved closer to the dog and stopped 1.6 m away from it. After 5 s as the UMOs stopped, the owner released the dog that could behave freely (e.g. approach and touch the UMOs and the balls attached to them) for 1 min. The UMOs stood still and did not react to the dogs' behaviour. Due to technical problems

the duration of the *Test phase* was less than 1 min in case of six subjects (mean time (s) ± SD 56.44 ± 8.04). We did not exclude these dogs, but we used the time from the moment the dog was released until the end as maximum time of the *Test phase* for the analysis of the latency data (see Behavioural variables and data analysis).

We counterbalanced between subjects the sides of the UMOs. For half of the subjects E1, for the other half of subjects E2 attached the ball to the UMO that demonstrated the chasing pattern.

**Behavioural variables and data analysis**

Tests were analysed with Solomon Coder 15.11.19.

*Observation phase*

Looking duration toward the chasing or independent demonstrations (%) is the looking duration toward the UMOs (s) during the chasing or independent demonstrations (from the UMOs first deviation from the elliptical route until both UMOs stopped) divided by the total time of the given demonstration (s); this quotient is multiplied by 100.

*Test phase*

*First approach* (0/1): the UMO that the dog approached first. *First touch* (0/1): the ball attached to the UMO that the dog touched first. We scored each trial as 0 if the dog approached/touched first the UMO (or the ball attached to it) from the independent demonstration, and as 1 if the dog approached/touched first the UMO (or the ball attached to it) from the chasing demonstration.

*Latency of first approaches* (s): latency of approaching the UMOs after the owner let the dog go. *Latency of first touches* (s): latency of touching the balls attached to the UMOs after the owner let the dog go. *Latency of first grabs* (s): latency of grabbing the balls attached to the UMOs after the owner let the dog go.

For statistical analysis we used IBM SPSS Statistics 22 and R software version 3.2.4 (R Development Core Team (2008)).

We compared dogs' looking duration toward the chasing and independent demonstrations during the *Observation phase* with related-samples Wilcoxon signed rank test (IBM SPSS). By one-sample binomial test (0.5 chance level) we analysed whether dogs approached and touched first the UMOs (or the ball attached to them) from the chasing demonstration (IBM SPSS). We

used mixed-effects Cox regression (R coxme package) to compare the differences between the latencies of the first approaches, first touches and first grabs of the UMOs (or the balls attached to them). We used Cox regression to test whether dogs' behaviour was influenced of whether the chaser or the chased UMO was in the room in the *Test phase* (latency of approach, touch and grab) (IBM SPSS).

We used Generalized Linear Models (GzLMs) to analyse whether the movement of the UMOs (started to move first, stopped later), or their potential different distances from the dog in the *Test phase* had an effect on dogs' first approach of the UMOs (IBM SPSS).

Inter-observer reliability for the looking duration (%) variable was tested on a random subsample of the recordings (20 % of the subjects) by an independent observer (Nikolett Czinege) (mean ± SD Cronbach's alpha was 0.703 ± 0.101).

### 4.3.2. Results

Related-samples Wilcoxon signed-rank test showed that dogs' looked at both demonstrations for equally long durations during the *Observation phase* (Looking at the chasing demonstration: mean (s) ± SD 76.122 ± 20.623; Looking at the independent demonstration: mean (s) ± SD 73.102 ± 13.618; Related-samples Wilcoxon signed-rank test: N = 24, z = -1.257, p = 0.209).

With mixed effects Cox regression, we found significant difference in the latency of first approach of the UMOs, and the latency of first touch and first grab of the balls attached to the UMOs. Dogs approached the UMOs from the chasing demonstration with approximately 4.4 times higher chance within a given time, than the UMOs from the demonstration of the independent motion (Log-likelihood comparison: $\chi^2 = 14.475$; $p < 0.001$; exp(β)[95% CI] = 4.359[2.11; 9.02]; $p < 0.001$) (Figure 4.21a). Also, dogs touched with approximately 4.3 times higher chance within a given time the ball attached to the UMOs from the chasing demonstration, than the ball attached to the UMOs from the demonstration of the independent motion (Log-likelihood comparison: $\chi^2 = 13.619$; $p = 0.001$; exp(β)[95% CI] = 4.26[2.02; 8.99]; $p < 0.001$) (Figure 4.21b). We also found that dogs grabbed the ball from the UMOs that demonstrated the chasing pattern with approximately 6.3 times higher chance within a given time, than from the UMOs that demonstrated the independent movement (Log-likelihood comparison: $\chi^2 = 10.509$; $p < 0.001$; exp(β)[95% CI] = 6.325[2.21; 18.13]; $p < 0.001$) (Figure 4.21c).

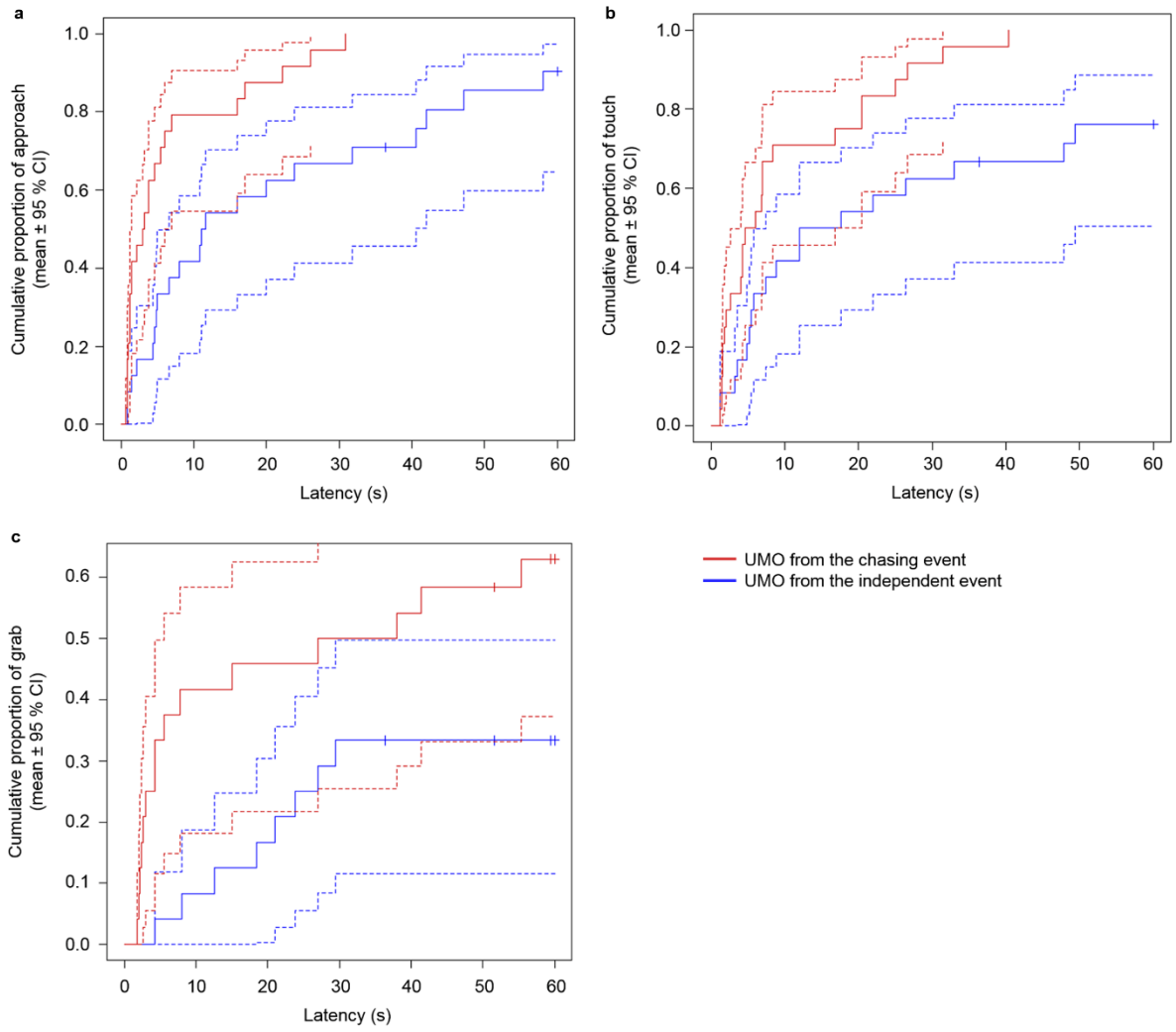


**Figure 4.21.** Latencies of (a) first approach of the UMOs, (b) first touches and (c) first grabs of the balls attached to the UMOs. The figures show the cumulative proportion of individuals presenting the given behaviour at a given time (mixed effects Cox regression). Full lines indicate the mean; dotted lines indicate the 95 % CI. Blue lines represent UMOs from the chasing event, while red lines indicate UMOs from the independent event.

Based on the results of the one-sample binomial test (0.5 chance level), dogs approached and touched the balls attached to the UMOs from the chasing demonstration significantly more often for the first time (approach: p = 0.002; touch: p = 0.002; Figure 4.22).

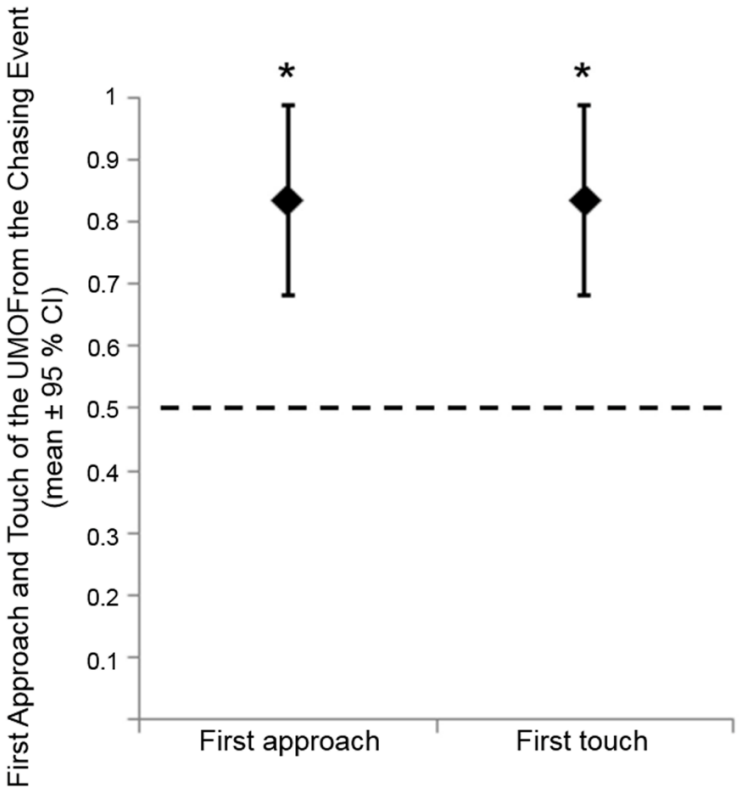


**Figure 4.22.** Dogs' first approach and first touch of the UMOs in the Test phase. The dashed line represents the 0.5 chance level. The value 0 represents the UMOs from the independent demonstration and the value 1 the UMOs from the chasing demonstration. * $p < 0.01$

Dogs' behaviour was independent of whether the chaser or the chased UMO was in the room in the *Test phase* (Cox regression: approach, $\exp(\beta) = 1.521$, p = 0.331; touch, $\exp(\beta) = 1.776$, p = 0.183; grab, $\exp(\beta) = 2.104$, p = 0.161).

We found that dogs' first approach of the UMOs were not influenced by which of the UMOs started to move first and stopped later when they moved closer to the dog in the *Test phase*. The difference in their distances from the dog also did not have an effect (GzLM: Moved first, $\chi_2^2 = 0.863$, p = 0.650; Stopped later, $\chi_2^2 = 9.15 \times 10^{-7}$, p = 1.000; Closer, $\chi_2^2 = 0.187$, p = 0.911).

### 4.3.3. Discussion

It seems that overall dogs were more interested in the UMOs from the chasing demonstration; they approached these UMOs sooner, and also touched and took away the balls attached to these agents earlier; independently of their role as chaser or chasee. We propose that dogs' behaviour reflect the recognition of the chasing pattern, and as a result they considered these UMOs as potential interactive partners. It is also a plausible explanation that dogs showed such preference, because during their daily lives both the balls and the chasing pattern can be associated with playing. This explanation also supports the recognition of the dependent motion pattern as chasing.

Subjects' preference between two stimuli is often measured by the duration of subjects' look at the stimuli. We found that dogs' looking duration did not differ between the demonstrations of the movement patterns, thus it can be raised that they did not prefer any of them. However, we suggest that differences/similarities in the looking time toward stimuli are most reliable when the stimuli are displayed simultaneously, and as a result subjects need to divide their attention between them. In that case we would expect that they spend more time looking at the stimulus they are more interested in. In the present study, we showed only one motion pattern at a time to dogs, thus there was no cost of looking at the less interesting pattern. We suggest that dogs' similar looking duration toward the dependent and independent motion patterns does not indicate the lack of preference or recognition in this specific case.

The novel method applied here can be a useful approach to study the spontaneous recognition of animacy for several reasons. Considering that subjects behave freely during the Test phase, they can engage in direct interaction with the agents (although these do not react to dogs' behaviour), which allows the assessment of a wider range of behaviour, including preference of one or the other UMO. We propose that this method offers a more direct measure of the perception of animacy because subjects have the chance to initiate an interaction. Also, in former studies that examined the duration of looking at the stimuli (e.g. Rochat et al. 1997; Abdai et al. 2017), the recognition of the dependent motion pattern was claimed indirectly (the recognition of the dependent pattern was claimed based on the longer looking toward the independent pattern). However, in the present study the conclusions were drawn from direct measurement of subjects' behaviour, from their preference toward the agents that demonstrated the chasing pattern (see also Mascalzoni et al. 2010; Rosa-Salva et al. 2016). We suggest that the present data provide stronger evidence on the presence of the phenomenon. Our novel method serves better the call from other researchers who suggested that by studying participants' implicit interactive behaviour, more objective data can be obtained, thus it may be

a more suitable way to test the perception of animacy (Gao et al. 2010; Gao and Scholl 2011; van Buren et al. 2016). In line with this, here we also investigated whether the observation of the dependent motion pattern performed by inanimate agents would have an effect on subjects' behaviour. In addition, our new method does not require initial training (cf. Goto et al. 2002; Atsumi and Nagasaka 2015), thus subjects do not habituate to the demonstrated patterns which could have an impact on their behaviour.

## 4.4. General discussion of animacy perception

Based on these findings, we conclude that dogs, similarly to human infants and adults can perceive animacy based on simple motion cues in different situations. The results also confirm, that although there are similarities in the perception of dogs and humans regarding this domain, there are subtle and more emphasized differences between the two species as well. However, more studies are required to explore these better before drawing conclusions.

As mentioned above, researchers found that different parameters of the motion can influence animacy perception in humans (e.g. Szego and Rutherford 2007; Gao et al. 2009; Gao and Scholl 2011; Frankenhuis et al. 2013; Meyerhoff et al. 2013); some researchers also found evidence that contextual information has an effect as well (Tremoulet and Feldman 2006; Gao et al. 2010; Parovel et al. 2018). The perceived characteristic of the motion may change not only by major differences (all-or-none, e.g. presence of directionality), but also depends on the values of the parameters (e.g. changing speed step-by-step). We propose that a specific motion pattern may give rise to the percept of animacy only within a specific range of the values of the parameters (cf. categorical perception; e.g. Eimas et al. 1971; Harnad 1987; Roberson and Davidoff 2000; Fugate 2013). Although in non-human species there is scarce evidence on animacy perception (but see Mascalzoni et al. 2010; Rosa-Salva et al. 2016), the effect of parameter settings should be important to take into account in future investigations. When studying non-human species, not only the experimental paradigm used (e.g. projected video vs. live demonstration by UMOs) can influence the results, but it is possible that different parameter settings may have an effect on perception as well. Our results regarding the presence of directionality support this notion, which is interesting considering that we only changed one single element of the stimuli. Although it should be noted that directionality is an important and easy to notice feature, which can only be changed categorically and not gradually. Thus we suggest that this aspect should be taken into consideration in studies conducted with non-human

species, and in case of seeming absence of the phenomenon, different parameter settings should be applied.

Differences in the processing of visual information or sensitivity to the characteristics of motion may cause differences between species; but differences in ecological relevance cannot be excluded. Species with different strategies (e.g. social vs. non-social species, herbivores vs carnivores) may also have different criteria of attributing animacy spontaneously to unfamiliar agents based on its motion characteristics. For example, the roles of herbivores and carnivores in the natural environment as preys and predators may have a strong influence on their perception of a movement pattern such as chasing, and they are more attentive to individuals with opposite roles. We propose that herbivores may be prone to be more attentive to a chaser agent; in contrast, carnivores might be more sensitive or show more interest toward the chasee.

Using an ethological approach to the phenomenon, we have already discussed that quick perception of animate entities is important for survival (see Section 4). In contrast to the broad literature in humans, the phenomenon has only been investigated in a few non-human species, thus we know little about animacy perception from the viewpoint of evolution. However, it seems that a phylogenetically distant species, domestic chicken also shows sensitivity to motion cues indicating animacy, and our results with dogs also suggest that this skill might emerge early during evolution. However, common evolutionary origin has not yet been proven. Regarding the development of animacy perception, we only have data in humans and domestic chicken; research on both species suggest that animacy perception may be present from birth. Further, studies with human infants suggest that infants from at least five months of age (cf. with three-month-olds) shows similar perception to that of adult humans (Rochat et al. 1997). However, differences between the age groups might be an artefact of the method used or the result of other factor (see e.g. Helo et al. 2016; Galazka and Nyström 2016). Unfortunately, data on its underlying mechanism is missing (see Section 3 for the theoretical debate around it), despite it would be an important step not only from the comparative point of view, but also for studies in related research areas (e.g. autism spectrum disorder; Abell et al. 2000; McAleer et al. 2011; Vanmarcke et al. 2017).

Here we applied two different methods to investigate the phenomenon in dogs. Projected stimuli allowed us to compare our results to previous findings in human infants (Rochat et al. 1997), and also to compare directly the behaviour of dogs and adult humans. Previous findings show that dogs' behaviour can be studied by applying projection of the stimuli, for example, dogs are able to use video recording as source of information in two-way choice tests (e.g. Pongrácz et al. 2003; Péter et al. 2013). This method is highly advantageous because it

facilitates reproducibility and repeatability of the experiments, and also enables the more flexible manipulation of the stimulus (Péter et al. 2013). This method is widely used in some other species as well (e.g. pigeons, Goto et al. 2002; domestic chicken, Jones et al. 1996; three-spined stickleback (*Gasterosteus aculeatus*), Rowland 1995; zebra finch (*Taeniopygia guttata*), Adret 1997; for a review see D'Eath 1998); however, it may not be the best approach to study the behaviour of non-human species, considering that projected images and videos are far from their natural set of visual inputs (see domestic hens, D'Eath and Dawkins 1996; for reviews about the use of video playbacks in studying animal behaviour, see D'Eath 1998; Fleishman and Endler 2000). Thus failing to show animacy perception in some species (see Section 4) may be the result of the method used, and not the abilities of the tested species. The novel methodological approach we introduced may help to overcome this issue by allowing a closer to natural situation, that can be conducted in their natural habitat as well. We propose that the use of UMOs can be applied widely among species to study the phenomenon that would allow more direct comparison of their abilities. Nowadays more and more robots are available, in cases of which many parameters of the movement (e.g. speed) can be set previously or the routes can be set beforehand. We believe that technological advances enable the refinement of our method to be able to control better for many parameters of the motion in the future and to be able to apply better suited robots based on the studied species.

# 5. APPLICATION OF OUR FINDINGS IN RESEARCH

Research presented here can provide useful input for investigations in related areas. Here we would like to provide a short overview of potential applications of our investigations in social evaluation, jealousy and animacy perception.

Jealousy is one of the leading causes of homicide in humans across cultures (e.g. Harris 2003; Harris and Darby 2003). It has been described as one of the main motives of non-accidental homicides not only in Western cultures, but also in, for example, Bhil people (India), the Basoga culture (Uganda, Africa), the Ifugaos (Philippines), and in Native Americans as the Navajo or Apache (e.g. Betzig 1989; Felson 1997; Harris 2003; Harris and Darby 2003). Another important issue is sibling rivalry originating from jealousy (when the sibling is considered as a rival from the viewpoint of relationship with the parents), which leads to verbal and physical aggression in many households (Felson 1983; Volling et al. 2013). In the USA it has been reported that more than 50 % (up to even 86 %) of intrafamily violence and abuse is sibling violence (Hoffman and Edwards 2004; Eriksen and Jensen 2006; Kettrey and Emery 2006; Khan and Cooke 2013), and it can lead to siblicide as well (Dawson and Langan 1994; Salmon and Hehman 2014). It has been debated whether jealousy emerging in different relationships (e.g. romantic relationship, friendship or among siblings) can be traced back to the same process (see Harris and Darby 2003; Volling et al. 2013). Thus research on the evolutionary origin of jealousy can serve important information about the phenomenon.

Jealous behaviour displayed by dogs also poses an important threat. Dog is a popular pet species, and as their number has grown in human households, dog-dog and dog-human aggression has become more and more important issue. Thus understanding more about jealous behaviour, its mediating factors and possible signs of it can help to avoid accidents and facilitate to develop behavioural therapy (see also Cook et al. 2018). In case of different underlying processes of behaviour problems in dogs, different behavioural therapies are suggested. Our findings on the emergence of jealous behaviour in dogs support that in case of the arrival of a new dog or a newborn infant into the family, dog's emerging behaviour problems should be regarded as manifestations of jealous behaviour.

These research areas may also contribute to the advancement of social robotics. One of the challenges of social robotics is how to develop robots that are capable of functionally meaningful social interactions with humans (Fong et al. 2003; Miklósi and Gácsi 2012; Miklósi et al. 2017). From this point of view, the Uncanny Valley effect (Mori 1970) is an important

issue. Mori (1970) suggested that close, but not perfect resemblance to humans leads to aversion to the robot; however, results of studies investigating the phenomenon are not unequivocal (Seyama and Nagayama 2007; MacDorman et al. 2009; Saygin et al. 2012; Abdai et al. in press). Miklósi et al. (2017) argued that similarity of robots to human physical appearance and behaviour should not be the aim, instead robots should have features optimal for their function. It has further been suggested that human-animal interactions can provide important information on robot design regarding behaviour (e.g. Miklósi and Gácsi 2012; Miklósi et al. 2017). Thus separation of the embodiment and behaviour of robots seems to be an important step; however, it is an interesting question how to facilitate the acceptance of robotic agents by humans. Miklósi et al. (2017) suggested that robots become social partners if they are able to engage in appropriate social interactions, thus robots need to be able to show at least some basic social skills (e.g. responsiveness to learning or communication). We further suggest that animacy perception may facilitate the acceptance of robots as social partners. Perceptual animacy relies on the spontaneous perception of inanimate objects as animate based on simple motion cues, which can influence observers' behaviour (see Gao et al. 2009, 2010; van Buren et al. 2016), even in dogs (Abdai et al. 2017a). We propose that animacy perception, irrespectively of the embodiment and presence of complex social behaviour, may facilitate the perception of robots as animate that can serve as basis to accept them as an agent competent to be a social partner, thus establish the basis for humans' social behaviour displayed toward the robot.

Parameters of motion characteristics that elicit animacy perception can be also programmed into robots that may help the automatic identification of possible animate agents (or at least draw attention to them to investigate more thoroughly), and discrimination between animate and inanimate objects in the environment.

Studies on social evaluation and jealous behaviour may also be important aspects in social robotics. The former can help to display more sophisticated behaviour toward humans in the environment of robots (discrimination between prosocial and antisocial humans); which may help in situations when the robot needs assistance from a human (e.g. robot gets stuck at an obstacle). Behavioural traits and skills such as attachment may be useful to tighten the relationship even between humans and robots (see Miklósi and Gácsi 2012; Miklósi et al. 2017), and jealous behaviour may also contribute to this. Programming "weak form" of jealous behaviour (e.g. some elements like "calling the attention of the human partner") may also facilitate the maintenance of the human-robot relationship that can be modelled based on the behaviour of dogs (see Miklósi and Gácsi 2012; Miklósi et al. 2017).

# 6. CONCLUSION

In the dissertation, I discussed *social evaluation*, *jealous behaviour* and *animacy perception* separately to provide deeper perspectives about dogs' ability to represent third-party interactions.

Findings about animacy perception showed that dogs are able to recognize the dependent movement of two inanimate objects as an interaction among them, relying solely on motion characteristics. We further found that dogs are able to assess the nature of interaction between two individuals (jealous behaviour). Thus dogs are able to take into consideration information gathered in third-party social interactions in at least two different situations. They are able to determine different features of the interacting agents, evaluate possible relationship between them accurately (e.g. chasing each other, or whether the interaction among the valued social partner and another agents threatens the relationship), and use this information to direct their future behaviour accordingly toward these agents (e.g. higher interest in animate, than in inanimate agents or displaying behaviour that facilitate to maintain the important social relationship).

Eavesdropping can contribute to fitness and survival in different contexts, depending on the social environment of the species. For example, in birds the protection of territory from intruders is crucial (e.g. great tits; Peake et al. 2002), and in non-human primates the assessment of social relationships (including hierarchy) within the group members is important (e.g. baboons; Cheney and Seyfarth 2004; see Chapter 1). However, it is still an open question whether social eavesdropping in different contexts (and species) relies on the same mental mechanisms.

In different species social eavesdropping develops early (may even be present from birth) (animacy perception: Rochat et al. 1997; Mascalzoni et al. 2010; Di Giorgio et al. 2017; social evaluation: Hamlin et al. 2007, 2010; jealousy: Hart and Carrington 2002), although changes in behaviour during development have been found (animacy: Rochat et al. 1997; social evaluation: Hamlin et al. 2011; Hamlin 2013b, 2014). Findings suggest that the ability to eavesdrop in indirect interactions is present in phylogenetically distant species; however, considering the above issues, we cannot make conclusions regarding its evolutionary origin, especially regarding its presence in very different contexts. From one point of view, this skill can be considered as an evolutionarily ancient skill (see Mascalzoni et al. 2010 for animacy perception in chicks); but it cannot be excluded that its emergence is the result of convergent evolution.

Research on different species would be important to gain more information on the phenomenon, but ecological relevance should not be neglected during investigation, neither from the viewpoint of method, nor when drawing conclusions and comparing different species.

## ACKNOWLEDGEMENT

As stated in the dissertation, the existence of helping behaviour that increases the fitness and survival of others at a cost to the helper (seemingly without any benefit to them), puzzled many researchers in the past. Well, I have had the luck to work with many people throughout the past few years, who will not help the job of evolutionary biologists.

First of all, I would like to thank my supervisor, Ádám Miklósi for teaching me to always see the broader picture, for always pushing me to think critically, for not letting me be too stubborn, for almost always having 15-30 minutes whenever I said: "*Can I have just one question? I swear it will only take about 2 minutes…*", and for being a great example of what a supervisor should be like. In sum, for everything.

I would also like to thank Bence Ferdinandy, Tamás Faragó, and Antal Dóka for all their help, especially for not killing me when I asked their help in the exact same thing for the 100$^{th}$ time. I also appreciate the help of Ákos Pogány, and I thank him for teaching me many different ways to normalize my data. It is, and will always be amazingly useful to me. And last, but not least, I would like to thank Cristina Baño Terencio for helping me in most of these studies, and for being able to bear with me as a supervisor.

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## PUBLICATIONS INCLUDED IN THE DISSERTATION

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# APPENDIX

**Table A1.** Data of subjects measured in: *3.1 Experimental investigation of jealous behaviour in dogs*. Orange colours indicate the subject dogs; yellow colour indicates the test partners (familiar dog).

| Dog ID | Breed | Age (year) | Sex | Dog ID | Breed | Age (year) | Sex |
|---|---|---|---|---|---|---|---|
| 1 | Staffordshire Bull Terrier | 11 | female | R1 | Staffordshire Bull Terrier | 11 | female |
| 2 | Mongrel | 9.5 | female | R2 | German Shepherd | 9.5 | female |
| 3 | Mixed (Pumi-Puli) | 10 | female | R3 | Miniature Schnauzer | 10 | female |
| 4 | Mongrel | 7 | male | R4 | Golden Retriever | 7 | male |
| 5 | Mongrel | 2 | male | R5 | Mongrel | 2 | male |
| 6 | Mongrel | 3.5 | male | R6 | Kuvasz | 3.5 | male |
| 7 | Mongrel | 6 | female | R7 | Chihuahua | 6 | female |
| 8 | Pit Bull Terrier | 1.5 | male | R8 | Mongrel | 1.5 | male |
| 9 | Mongrel | 3 | male | R9 | Mongrel | 3 | male |
| 10 | Mongrel | 5 | female | R10 | Mongrel | 5 | female |
| 11 | Hungarian Vizsla | 6 | male | R11 | Hungarian Vizsla | 6 | male |
| 12 | Collie | 3 | female | R12 | Mongrel | 3 | female |
| 13 | Basset Hound | 1.5 | female | R13 | Bolognese | 1.5 | female |
| 14 | Belgian Shepherd (Groenendael) | 8 | female | R14 | Sheltie | 8 | female |
| 15 | Yorkshire Terrier | 7 | male | R15 | Giant Schnauzer | 7 | male |
| 16 | Mongrel | 4 | female | R16 | Mongrel | 4 | female |
| 17 | Mongrel | 3 | female | R17 | Labrador Retriever | 3 | female |
| 18 | Hovawart | 6 | female | R18 | Hovawart | 6 | female |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| 19 | Border Collie | 4 | male | R19 | Border Collie | 4 | male |
| 20 | Mongrel | 3 | male | R20 | Mongrel | 3 | male |
| 21 | Boxer | 3 | female | R21 | Boxer | 3 | female |
| 22 | Mongrel (Malinois) | 4 | male | R22 | Mongrel | 4 | male |
| 23 | Mongrel (Pumi) | 2 | female | R23 | Mongrel (German Shepherd) | 2 | female |
| 24 | Wirehaired Hungarian Vizsla | 5 | female | R24 | Longhaired Dachshund | 5 | female |

**Table A2.** Data of dogs measured in: *Comparative approach to the perception of animacy*. In the *ID of displayed video* 'R' stands for right and 'L' for left, indicating the side of the Chasing motion pattern in Trial 1 and 2 (respectively).

| Dog ID | Breed | Age (year) | Sex | ID of displayed video |
|---|---|---|---|---|
| 1 | Golden Retriever | 6 | male | 1_016_RL |
| 2 | Mongrel | 4 | female | 1_009_RL |
| 3 | Shiba Inu | 6 | female | 1_016_LR |
| 4 | Terrier | 2 | male | 1_007_RL |
| 5 | Mongrel | 11 | male | 1_009 LR |
| 6 | West Highland White Terrier | 8 | female | 1_055_RL |
| 7 | Mongrel | 3 | male | 1_056_LR |
| 8 | Mongrel | 15 | male | 1_056_RL |
| 9 | Miniature Poodle | 5 | male | 1_068_RL |
| 10 | Mongrel | 5 | female | 2_012_LR |
| 11 | Belgian Shepherd (Malinois) | 4.5 | female | 2_012_RL |
| 12 | Mongrel | 5 | female | 2_020_LR |

| | | | | |
|---|---|---|---|---|
| 13 | Mongrel | 6 | male | 2_020_RL |
| 14 | Border Collie | 9 | female | 2_023_LR |
| 15 | Pekingese | 9 | male | 2_023_RL |
| 16 | Belgian Shepherd (Groenendael) | 8 | female | 2_032_LR |
| 17 | Mongrel | 1.5 | female | 2_032_RL |
| 18 | Mongrel | 13 | male | 2_041_RL |
| 19 | Hungarian Vizsla | 1.5 | female | 2_051_LR |
| 20 | American Pit Bull Terrier | 7 | female | 2_051_RL |
| 21 | Spitz | 3 | male | 2_059_RL |
| 22 | Mongrel | 3 | female | 2_074_LR |
| 23 | Yorkshire Terrier | 8 | male | 2_074_RL |
| 24 | Parson Russell Terrier | 7 | female | 1_007_LR |
| 25 | Mixed (Mudi-Kuvasz) | 1.29 | male | 1_053_LR |
| 26 | Golden Retriever | 5.5 | female | 1_053_RL |
| 27 | English Cocker Spaniel | 3.5 | female | 2_059_LR |
| 28 | English Cocker Spaniel | 3.5 | male | 2_041_LR |
| 29 | Staffordshire Bull Terrier | 11 | female | 1_055_LR |
| 30 | Staffordshire Bull Terrier | 8 | male | 1_068_LR |

**Table A3.** Data of humans measured in: *Comparative approach to the perception of animacy*. In the *ID of displayed video* 'R' stands for right and 'L' for left, indicating the side of the Chasing motion pattern in Trial 1 and 2 (respectively).

| Human ID | Age (year) | Sex | ID of displayed video |
|---|---|---|---|
| 1 | 20 | woman | 1_007_LR |
| 2 | 20 | woman | 1_007_RL |
| 3 | 24 | woman | 1_009_LR |
| 4 | 23 | woman | 1_009_RL |
| 5 | 25 | woman | 1_016_LR |
| 6 | 25 | woman | 1_016_RL |
| 7 | 20 | woman | 1_053_LR |
| 8 | 25 | man | 1_053_RL |
| 9 | 21 | woman | 1_055_LR |
| 10 | 25 | woman | 1_055_RL |
| 11 | 24 | man | 1_056_LR |
| 12 | 24 | man | 1_056_RL |
| 13 | 24 | man | 1_068_LR |
| 14 | 22 | man | 1_068_RL |
| 15 | 23 | man | 2_012_RL |
| 16 | 20 | woman | 2_020_LR |
| 17 | 20 | woman | 2_020_RL |
| 18 | 20 | woman | 2_023_LR |
| 19 | 21 | woman | 2_023_RL |
| 20 | 22 | woman | 2_032_LR |
| 21 | 25 | man | 2_032_RL |
| 22 | 20 | man | 2_041_LR |
| 23 | 20 | woman | 2_041_RL |

| | | | |
|---|---|---|---|
| 24 | 19 | woman | 2_051_LR |
| 25 | 19 | woman | 2_051_RL |
| 26 | 19 | man | 2_059_LR |
| 27 | 20 | woman | 2_059_RL |
| 28 | 20 | woman | 2_074_LR |
| 29 | 23 | man | 2_074_RL |
| 30 | 25 | man | 2_012_LR |

**Table A4.** Data of dogs measured in: *Importance of directionality in the perception of animacy*. In the *ID of displayed video* 'R' stands for right and 'L' for left, indicating the side of the Chasing motion pattern in Trial 1 and 2 (respectively).

| Dog ID | Breed | Age (year) | Sex | ID of displayed video |
|---|---|---|---|---|
| 1 | Mongrel | 3.5 | female | 2_020tri_LR |
| 2 | Siberian Husky | 1.5 | female | 1_007tri_RL |
| 3 | Mongrel | 2.5 | male | 1_007tri_LR |
| 4 | Siberian Husky | 2 | male | 2_059tri_RL |
| 5 | Basset Hound | 2.5 | female | 2_074tri_LR |
| 6 | Mudi | 2.5 | male | 2_059tri_LR |
| 7 | Berger de Beauce | 1 | male | 1_055tri_RL |
| 8 | Mongrel | 1 | male | 1_053tri_LR |
| 9 | Mongrel | 4 | female | 2_012tri_LR |
| 10 | Papillon | 6 | female | 1_016tri_RL |
| 11 | Mongrel | 1 | female | 1_009tri_RL |
| 12 | Mongrel | 8.5 | male | 1_016tri_LR |
| 13 | Mongrel | 1 | male | 2_074tri_RL |
| 14 | Border Collie | 2 | female | 2_051tri_LR |
| 15 | Mongrel | 7.5 | female | 2_012tri_RL |

| | | | | |
|---|---|---|---|---|
| 16 | Dachshund | 6 | male | 2_023tri_RL |
| 17 | Border Collie | 10 | female | 1_053tri_RL |
| 18 | Mongrel | 4 | male | 1_009tri_LR |
| 19 | Mongrel | 3 | female | 2_041tri_RL |
| 20 | Wire-Haired Dachshund | 1.5 | male | 1_055tri_LR |
| 21 | Labrador Retriever | 5 | male | 2_041tri_LR |
| 22 | Mongrel | 7 | female | 1_068tri_RL |
| 23 | Pug | 2 | male | 2_051tri_RL |
| 24 | Golden Retriever | 3 | female | 2_023tri_LR |
| 25 | Dogo Argentino | 5 | female | 2_032tri_LR |
| 26 | Mongrel | 6 | female | 1_056tri_RL |
| 27 | German Shepherd | 11 | male | 1_056tri_LR |
| 28 | Weimaraner | 9 | male | 2_020tri_RL |
| 29 | Golden Retriever | 9 | male | 2_032tri_RL |
| 30 | French Bulldog | 1 | female | 1_068tri_LR |

**Table A5.** Data of humans measured in: *Importance of directionality in the perception of animacy*. In the *ID of displayed video* 'R' stands for right and 'L' for left, indicating the side of the Chasing motion pattern in Trial 1 and 2 (respectively).

| **Human ID** | **Age (year)** | **Sex** | **ID of displayed video** |
|---|---|---|---|
| 1 | 24 | woman | 1_007tri_LR |
| 2 | 23 | woman | 1_007tri_RL |
| 3 | 21 | woman | 1_009tri_LR |
| 4 | 22 | woman | 1_009tri_RL |
| 5 | 23 | woman | 1_016tri_LR |
| 6 | 21 | woman | 1_016tri_RL |
| 7 | 22 | woman | 1_053tri_LR |

| | | | |
|---|---|---|---|
| 8 | 24 | man | 1_053tri_RL |
| 9 | 21 | man | 1_055tri_LR |
| 10 | 22 | woman | 1_055tri_RL |
| 11 | 22 | man | 1_056tri_LR |
| 12 | 21 | man | 1_056tri_RL |
| 13 | 20 | woman | 1_068tri_LR |
| 14 | 19 | woman | 1_068tri_RL |
| 15 | 21 | woman | 2_012tri_LR |
| 16 | 22 | man | 2_012tri_RL |
| 17 | 22 | man | 2_020tri_LR |
| 18 | 21 | man | 2_020tri_RL |
| 19 | 21 | man | 2_023tri_LR |
| 20 | 22 | woman | 2_023tri_RL |
| 21 | 21 | woman | 2_032tri_LR |
| 22 | 22 | woman | 2_032tri_RL |
| 23 | 20 | woman | 2_041tri_LR |
| 24 | 21 | woman | 2_041tri_RL |
| 25 | 22 | woman | 2_051tri_LR |
| 26 | 20 | woman | 2_051tri_RL |
| 27 | 23 | woman | 2_059tri_LR |
| 28 | 23 | woman | 2_059tri_RL |
| 29 | 21 | woman | 2_074tri_LR |
| 30 | 23 | woman | 2_074tri_RL |

**Table A6.** Data of subjects measured in: *Novel approach to study animacy perception in non-human species*. *Pattern demonstrated first* indicates which motion pattern was demonstrated first to subjects in the Observation phase. *UMOs in Test phase* indicates the UMOs that were placed in the room from the chasing and independent events in the Test phase; CH-1 indicates the chasee (UMO-1), CH-2 indicates the chaser (UMO-2), IND indicates the UMOs from the Independent motion pattern (IND-1 is UMO-1, IND-2 is UMO-2). *Experimenter* indicates the experimenter who attached the ball to the UMO from the chasing event in the Test phase. *Side of chasing UMO* indicates the side to which the UMO from the chasing event was placed in the Test phase (L-left, R-right). Orange background indicates dogs who were tested with the smaller platform.

| Dog ID | Breed | Age (year) | Sex | Pattern demonstrated first | UMOs in Test phase | Experimenter | Side of chasing UMO |
|---|---|---|---|---|---|---|---|
| 1 | Mongrel | 5 | female | Independent | CH-1 & IND-1 | E2 | L |
| 2 | Mongrel | 5 | female | Independent | CH-1 & IND-1 | E2 | R |
| 3 | Belgian Shepherd (Malinois) | 4.5 | female | Chasing | CH-2 & IND-2 | E1 | L |
| 4 | Mongrel | 6 | male | Chasing | CH-1 & IND-1 | E2 | L |
| 5 | Pekingese | 9 | male | Independent | CH-2 & IND-2 | E1 | R |
| 6 | Border Collie | 9 | female | Independent | CH-2 & IND-2 | E1 | L |
| 7 | Miniature Poodle | 5 | male | Chasing | CH-1 & IND-1 | E2 | L |
| 8 | Mongrel | 7 | male | Chasing | CH-1 & IND-1 | E1 | R |
| 9 | Mongrel | 6 | female | Independent | CH-1 & IND-1 | E1 | R |
| 10 | Mongrel (Pumi) | 2 | female | Independent | CH-2 & IND-2 | E2 | R |
| 11 | Mongrel | 5.5 | male | Independent | CH-2 & IND-2 | E1 | L |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| 12 | American Pit Bull Terrier | 5.5 | female | Chasing | CH-1 & IND-1 | E1 | L |
| 13 | Pembroke Welsh Corgi | 1 | male | Independent | CH-1 & IND-1 | E1 | R |
| 14 | Mongrel | 2 | female | Chasing | CH-2 & IND-2 | E2 | L |
| 15 | Boxer | 1.5 | female | Chasing | CH-2 & IND-2 | E2 | R |
| 16 | Mongrel | 5 | male | Independent | CH-2 & IND-2 | E2 | R |
| 17 | Mongrel | 13 | male | Chasing | CH-2 & IND-2 | E1 | L |
| 18 | Pug | 4 | female | Chasing | CH-1 & IND-1 | E2 | R |
| 19 | Mongrel | 1.5 | female | Chasing | CH-1 & IND-1 | E1 | R |
| 20 | American Pit Bull Terrier | 7 | female | Independent | CH-1 & IND-1 | E1 | R |
| 21 | Mudi | 4.5 | female | Chasing | CH-2 & IND-2 | E2 | R |
| 22 | Schnauzer | 7 | female | Independent | CH-1 & IND-1 | E2 | L |
| 23 | Border Collie | 1.17 | male | Chasing | CH-2 & IND-2 | E1 | R |
| 24 | Hungarian Vizsla | 1.5 | female | Independent | CH-2 & IND-2 | E2 | L |

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# ADATLAP

**a doktori értekezés nyilvánosságra hozatalához***

**I. A doktori értekezés adatai**

A szerző neve: Abdai Judit

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A doktori értekezés címe és alcíme: Interpretation of third-party social interaction in dogs

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A doktori iskola neve: Biológia Doktori Iskola

A doktori iskolán belüli doktori program neve: Etológia Doktori Program

A témavezető neve és tudományos fokozata: Miklósi Ádám, PhD, DSc

A témavezető munkahelye: Etológia Tanszék, Eötvös Loránd Tudományegyetem és MTA-ELTE Összehasonlító Etológiai Kutatócsoport

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Kelt: 2018. szeptember 4.

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